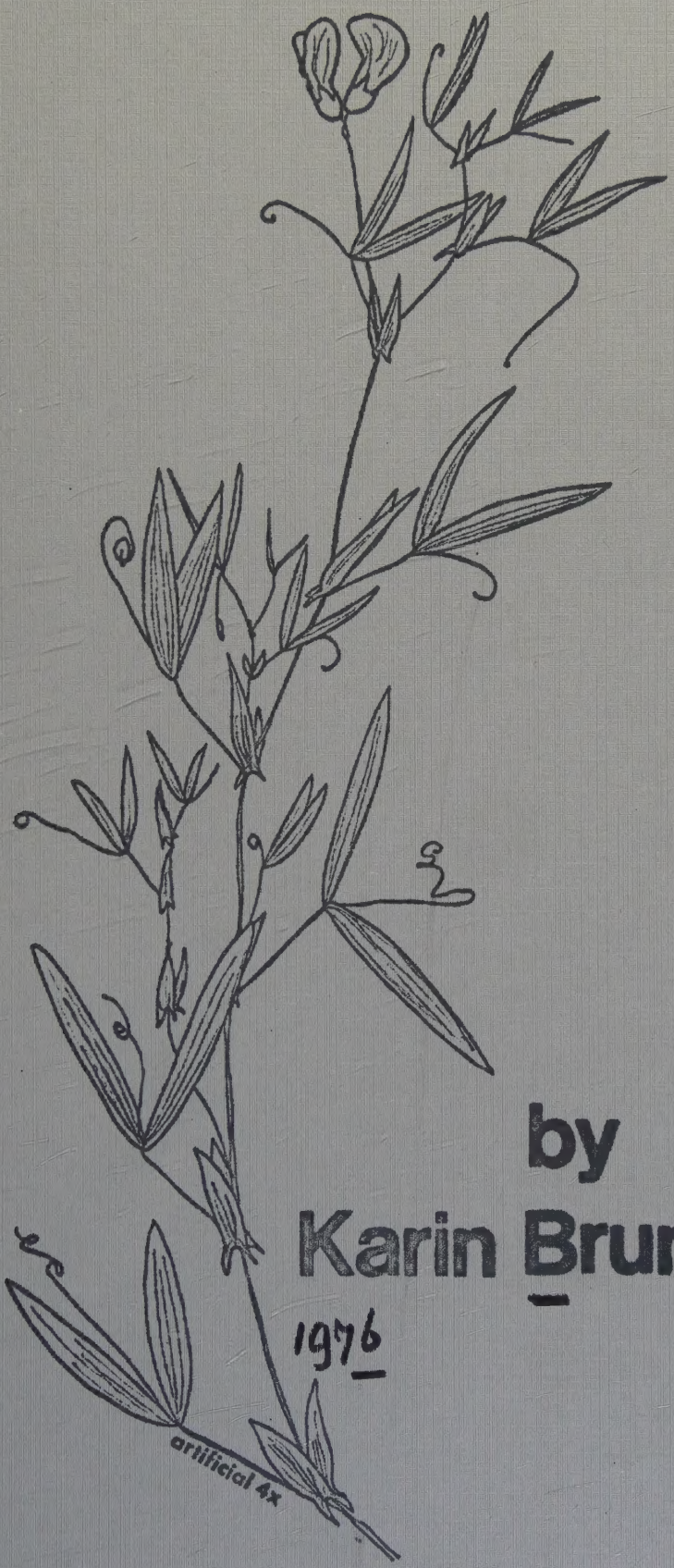
Lund 1976

BIOSYSTEMATICS IN THE LATHYRUS PRATENSIS COMPLEX



by
Karin Brunsberg

1976

BIOSYSTEMATICS IN THE LATHYRUS PRATENSIS COMPLEX

AV

KARIN BRUNSBERG

FIL. LIC. BL.

AKADEMISK AVHANDLING

som för avläggande av filosofie doktorsexamen vid Matematisk-Naturvetenskapliga Fakulteten vid Universitetet i Lund kommer att offentligen försvaras å föreläsningssalen vid Institutionen för Systematisk Botanik, måndagen den 5 april 1976 klockan 10.00.

BIOSYSTEMATICS IN THE LATHYRUS PRATENSIS COMPLEX

By Karin Brunsberg

DEPARTMENT OF PLANT TAXONOMY,
UNIVERSITY OF LUND,
Ö VALLGATAN 18—20
S – 223 61 LUND, SWEDEN

To my family

LUND 1976

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BIOSYSTEMATICS IN THE LATHYRUS PRATENSIS COMPLEX

C O N T E N T S

I INTRODUCTION 4

II TAXONOMIC SURVEY OF THE LATHYRUS PRATENSIS COMPLEX 5

III MATERIAL STUDIED 8

IV CHROMOSOME STUDIES 10

Chromosome numbers previously published 10

Material 10

Cytological technique 10

Somatic chromosome numbers in the present investigation 12

Aneusomaty, polysomaty and aneuploidy 15

Chromosome morphology 22

Male meiosis 22

V ISOLATION AND CROSSING EXPERIMENTS 30

Material and methods 30

Isolation experiments 30

Crossing experiments 32

Experiment in triploid Lathyrus pratensis 36

Conclusions 36

VI REPRODUCTIVE BIOLOGY 37

Flowering periods 37

Male fertility 37

Pollination and seed-setting 43

Seed germination and dispersal 45

Asexual reproduction 47

VII ARTIFICIAL POLYPLOIDS 49

BIOSYSTEMATICS IN THE LATHYRUS PRATENSIS COMPLEX

C O N T E N T S

I INTRODUCTION 4

II TAXONOMIC SURVEY OF THE LATHYRUS PRATENSIS COMPLEX 5

III MATERIAL STUDIED 8

IV CHROMOSOME STUDIES 10
Chromosome numbers previously published 10
Material 10
Cytological technique 10
Somatic chromosome numbers in the present investigation 12
Aneuploidy, polyploidy and euploidy 15
Chromosome morphology 22
Male meiosis 22

V ISOLATION AND CROSSING EXPERIMENTS 30
Material and methods 30
Isolation experiments 30
Crossing experiments 32
Experiment in triploid *Lathyrus pratensis* 36
Conclusions 36

VI REPRODUCTIVE BIOLOGY 37
Flowering periods 37
Male fertility 37
Pollination and seed-setting 43
Seed germination and dispersal 45
Asexual reproduction 47

VII ARTIFICIAL POLYPLOIDS 49

VIII GEOGRAPHIC DISTRIBUTION 52
Lathyrus pratensis 52
Lathyrus binatus 54
Lathyrus hallersteinii 55
Conclusions 55

IX THE OCCURENCE OF THE LATHYRUS PRATENSIS COMPLEX IN DIFFERENT PLANT SOCIETIES 56
Material and methods 56
Plant communities with Lathyrus pratensis 57
Plant communities with Lathyrus binatus 65
Plant communities with Lathyrus hallersteinii 65
Soil analyses 67

X MORPHOLOGICAL VARIATION 68
Material 68
Methods 70
Rhizomes and shoots 70
Leaves 72
Stipules 72
Epidermis and stomata 74
Plastids 76
Inflorescence and flowers 78
Calyx 81
Corolla 84
Pollen 84
Gynoecium 87
Pods and seeds 92
Conclusions 94

XI TAXONOMY 98
Treatment 100

XII THE PROBLEM OF AUTOPOLYPLOIDY 105
Autopolyploidy in Lathyrus pratensis 106
Conclusions 108

LITERATURE CITED 111

APPENDIX I Localities of spontaneous, cultivated material I
APPENDIX II Herbarium material examined XIV

VIII GEOGRAPHIC DISTRIBUTION 52
Lathyrus pratensis 53
Lathyrus vinetus 54
Lathyrus palustris 55
Conclusions 55

IX THE OCCURRENCE OF THE *LATHYRUS PRATENSIS* COMPLEX IN DIFFERENT PLANT SOCIETIES 56
Material and methods 56
Plant communities with *Lathyrus pratensis* 57
Plant communities with *Lathyrus vinetus* 65
Plant communities with *Lathyrus palustris* 65
Soil analyses 67

X MORPHOLOGICAL VARIATION 68
Material 69
Methods 70
Rhizomes and shoots 70
Leaves 72
Stipules 72
Epidermis and stomata 74
Pistils 76
Inflorescence and flowers 78
Calyx 81
Corolla 84
Pollen 84
Gynoecium 87
Pods and seeds 92
Conclusions 94

XI TAXONOMY 98
Treatment 100

XII THE PROBLEM OF AUTOTRIPLOIDY 105
Autotriploidy in *Lathyrus pratensis* 106
Conclusions 108

LITERATURE CITED 111

APPENDIX I Localities of spontaneous,cultivated material I
APPENDIX II Herbarium material examined XIV

I INTRODUCTION

The aim of the present study was to do a taxonomical revision of the *Lathyrus pratensis* complex and to discuss the possibility of autopolyploidy in the complex.

The study of the *L. pratensis* complex, which was carried out at the Institute of Systematic Botany, University of Lund, Sweden, is based upon herbarium material and living plants from Europe, cultivated under as similar conditions as possible in the Botanical Gardens, Lund, In all, about 500 samples with usually 3--10 plants per population were cultivated and closely studied. In addition, all accessible herbarium material of the *L. pratensis* complex from 56 herbaria was controlled. The investigation was carried out mainly during 1961--1968 and 1975.

The present work includes a cytological investigation with determination of the somatic chromosome numbers of all samples cultivated. Some examples of meiosis and karyotype analyses are also given. Isolation and crossing experiments are discussed. Geographical distribution and some examples of plant communities of taxa analysed are presented. In order to study the genetic and environmental modificative variation, the morphological investigation includes a comparison of the same plant material before and after 3--5 years of cultivation.

The study has been supported by grants from the Swedish Natural Science Research Council, The University of Lund, The Royal Physiographic Society of Lund, The Lund Botanical Society, The Swedish Academy and Carl-Bertl Nathhorst's Scientific Foundation. To all institutes, museums and persons that have contributed to the progress and completion of this study, I wish to express my sincere thanks.

II. TAXONOMIC SURVEY OF THE LATHYRUS PRATENSIS COMPLEX

The only existing monograph on the genus Lathyrus is that published by Alefeld (1861). Major regional revisions have been presented by Burkart (1935) for Argentina, Hitchcock (1952) for North America, Ball (1968) for Europe, Davis (1970) for Turkey and Bässler (1973) in his revision of section Orobus for Europe and Asia.

The taxonomic treatment of the genus and its subdivisions has varied. Linnaeus (1753) recognised two genera, Lathyrus and Orobus, which has been supported by several later authors, e. g. Döll (1843). Alefeld (1861) split Lathyrus into 8 separate genera. Most taxonomists, for instance Grenier & Godron (1848), Boissier (1872), Fritsch (1900), Ascherson & Graebner (1910), Davis (1970) and Czefranova (1971) have recognised one single genus, Lathyrus, subdivided into a number of sections. Bässler (1966) recognised one genus, Lathyrus, with two subgenera, Lathyrus and Orobus.

The L. pratensis complex has generally been included in sect. Orobastrum (Taub.) Boiss. In Bässler's system it constitutes a separate section Pratensis Bässl., within subgen. Orobus. Davis (1970) used a wider circumscription of sect. Pratensis including sect Eurytrichon Bässl. with three endemic Turkish species. The L. pratensis complex is a distinct and taxonomically well delimited group within the genus Lathyrus, which is evident e. g. from Bässler's treatment of the complex as a separate section. It is characterised by perennial growth, angled to terete stems, usually tendrillous leaves, 1-paired leaflets parallel-veined from the base, large ± unequally sagittate stipules, yellow flowers in few-flowered to many-flowered racemes, calyx teeth acuminate, unequal to ± equal in length, and style neither twisted nor dilated above.

The L. pratensis complex is indigenous to Europe, western and central Asia and northern Africa southwards to Ethiopia. Five species have been described within the complex viz. L. pratensis L., L. sepium Scop., L. hallersteinii Baumg., L. lusseri Heer ex

Koch, and L. binatus Pančić.

L. pratensis Linnaeus (1753) was described from material from Europe. It is distributed within the whole area of distribution of the group and also introduced in North America. L. pratensis (Fig. 1 A,B) is very variable and a great number of intraspecific taxa have been described, e. g. using differences in pubescence, size of leaves, stipules and flowers and the degree of angle of the stems (cf. Ascherson & Graebner 1910).

L. sepium Scopoli (1772) was described from material from the Goriza area in northern Italy. It is also recorded from two mountains in Austria. L. sepium was accepted as a species by Reichenbach (1830--1832) among others. It was reduced to a variety of L. pratensis by Alefeld (1861). Most authors have followed Alefeld or given it no taxonomic status, e.g. Beck von Mannagetta (1892) Marchesetti (1896--1897), Reichenbach & Beck de Mannagetta (1903), Schuster (1906), Ascherson & Graebner (1910), Hayek (1924--1927) and Grinţescu & Nyárády (1957). However, it was accepted as a species by Dalla Torre & Sarnthein (1909). L. sepium is characterised by ± glabrous leaves and stems, pubescent peduncle, and calyx teeth of ± equal length with the uppermost ones bent upwards.

L. hallersteinii Baumgarten (1816) was described from material from Csora in Roumania. In the literature the species has been recorded from Roumania, Yugoslavia and recently (Ball 1968) from Greece. Many taxonomists have accepted it as a distinct species, e. g. Schur (1866), Hayek (1924--1927), Grinţescu & Nyárady (1957), Bässler (1966) and Ball (1968) Rochel (1828), Reichenbach (1830--1832) Grisebach & Schenk (1852), Schuster (1906) and Ascherson & Graebner (1910) treated it as a variety of L. pratensis, and Alefeld (1861) did not mention it in his monograph on the genus. On herbarium sheets of this taxon he has written Orobus pratensis Döll. L. hallersteinii is characterised by being wholly glabrous by having broad stipules and leaves with tendrils, 1-sided racemes, calyx teeth of equal length and dark brown pods (Fig. 1D).

L. lusseri Heer ex Koch (1847, not validly published) was based on alpine material from the southern parts of the Alps. The description was short and the species has rarely been accepted but has sometimes been regarded as synonymous with L. pratensis var. grandiflorus Bogenhard (1850) from Germany and L. pratensis γ subalpinus Rouy (1899) from France. Schuster (1906) treated it as a synonym of L. sepium Scop. Löve & Löve (1956) suggested that tetraploid L. pratensis should be named L. lusseri. L. lusseri is characterised as ± glabrous with large flowers.

L. binatus Pančić (1874) was described on material from Mokra Gore in Serbia, Yugoslavia. It has later also been recorded from Bosna and Hercegovina. It was reduced to varietal level by Ascherson & Kanitz (1877), a treatment followed by Hayek (1924--1927). Ascherson & Graebner (1910) regarded it as a synonym of L. pratensis var. acirrhosus Beck. Bässler (1966) apparently did not accept it as a species as it was not mentioned as a member of his new section Pratensis, but Ball (1968) again accepted it at specific level. L. binatus is characterised by its small size, small leaves and stipules and few-flowered racemes (Fig. 1 C).

III. MATERIAL STUDIED

HERBARIUM MATERIAL

Apart from my own collections, material of the Lathyrus pratensis complex from 56 herbaria has been studied, viz. (abbreviations according to Holmgren & Keuken 1974): AAU, AMB, B, BEO, BERN, BM, BP, BR, BRA, BRLU, BUC, C, CL, COI, CP, FI, G, GB, GE, GRO, H, HAL, HUJ, ID, K, KIEL, L, LD, LE, LISU, LUB, LY, LZ, M, MA, MPU, MT, NBV, O, P, PR, PRC, S, SARA, SLO, SOM, TI, TK, TNS, U, UPS, W, WA, WU, Z and ZA.

The herbarium material studied represented the complex in the whole of Europe and in addition gave a good picture of the morphological variation in Asia. A few collections of L. pratensis from North America and North Africa were checked.

CULTIVATED MATERIAL

Spontaneous material (living plants and/or seed samples) from 509 populations were collected mainly by the author (1961 — 1965) in various parts of Europe during 8 months (Table 2). In addition spontaneous material was received from botanists in various parts of Europe. In a few cases seeds from herbarium material have germinated.

In the field 3 — 10 (— 40) live plants and/or seeds from about the same number of individuals were taken. Some shoots of every plant collected were dried. The author has tried to get a representative geographical distribution of the collections. However, the material from Poland and USSR, for example, was more limited than in other parts of Europe. The investigations have been more extensive in the regions where both diploid and tetraploid L. pratensis occur. The cultivated material was selected to represent as much of the wide ecological range of the species complex as possible. Plants were collected from sea level up to 2100 m.

The material was cultivated in the Botanical Gardens, University of Lund. The plants were grown in sterilised standard soil (about 50 % sand and 50 % humus) out of doors under as uniform conditions as possible. The experimental material is listed in Appendix I.

Fig. 1. A: Lathyrus pratensis 2n=28 (PPC:5). -- B: L. pratensis 2n=14 (PLY:3). -- C: L. binatus 2n=14 (BAA:5). -- D: L. hallersteinii 2n=14 (HBB:6).

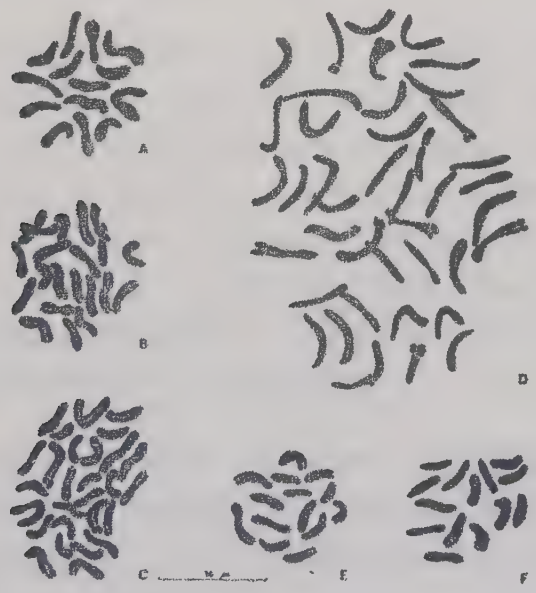


Fig. 2. Root-tip mitoses (microtome-cut preparations) of Lathyrus pratensis (A--D), L. binatus (E) and L. hallersteinii (F). -- A: PEF:1 2n=14. -- B: PCG:12 2n=21. -- C: POJ:1 2n=28. -- D: PPR:1 2n=42. -- E: BAB:12 2n=14. -- F: HBD:5 2n=14.

IV. CHROMOSOME STUDIES

CHROMOSOME NUMBERS PREVIOUSLY PUBLISHED

Chromosome numbers have been reported for more than 60 *Lathyrus* species (Bolkhovskikh et al. 1969, Brunsberg 1965, Cave 1956--1964, Darlington & Wylie 1955, Datta 1955, Fedorov 1969, Fouzdar & Tandon 1972, Hitchcock 1952, Löve & Löve 1956, Roy & Singh 1967, 1968, Simonet 1932). The basic number is x=7. Only two aneuploid species are known (*L. davidii* Hance 2n=16, *L. subrotundus* Maxim 2n=12). As in the closely related genera *Vicia*, *Lens* and *Pisum* very few polyploids have been found.

In *L. pratensis* 2n=14 and 28 have been recorded several times. Triploids and hexaploid plants have occasionally been found. A survey of recorded chromosome numbers is given in Table 1.

MATERIAL

Chromosome numbers were determined for the majority of the plants cultivated. Meiotic studies were performed on material cultivated outdoors only. Generally, the same plant was examined several times.

CYTOLOGICAL TECHNIQUE

The methods that were found to be the most satisfactory for each type of examination are given below.

The root tips were pretreated up to 16 hours in water at 5° C to contract the chromosomes. The tips were then fixed in the Svalöv modification of Navashin's fixative (Müntzing 1933) for more than one week, embedded in paraffin wax and sectioned at 15 µm. Before staining, the slides were pretreated for about 3 hours with a 10 % solution of citric acid (Lövkvist 1956). They were stained in a 1 % aqueous solution of crystal violet for about 16 hours. The preparations were mounted in Permount.

For more detailed studies of the somatic chromosomes, the squash technique described by Östergren & Heneen (1962) was used with a modified pretreatment (0,5 % colchicine at + 18° C for half an hour).

Male meioses were studied in squash preparations. Young flower buds were fixed in absolute alcohol, chloroform and glacial acetic acid (6:3:1) and stained in aceto-orcein or in Feulgen.

Table 1. The somatic chromosome numbers of *Lathyrus pratensis*, *L. binatus* and *L. hallersteinii* previously reported. The names of the countries are abbreviated in accordance with Flora Europaea (TUTIN et al 1964). [1]Number not verified.

Taxa	2n	Origin	Author
L. pratensis	14	Rs	MELDERIS & VIKSNE (1931)
	14	?	SENN (1938 a, b)
	14	Au, Cz, Da, Fa, Fe, Ga, Ge, Ju, Su	LARSEN (1953, 1954, 1957)
	14	Is, NW Eu	LÖVE & LÖVE (1956)
	14	Fe, Ga, Ge	SIMOLA (1964)
	14	Au, Da, Ge, He, Ju, Rm, Su	BRUNSBERG (1965)
	21	Fe	SIMOLA (1964)
	21	Su	BRUNSBERG (1965)
	28	Br	MARKS (1950)
	28	Br, Ga, Ho, Hs, It, Ju, Channel Islands	LARSEN (1953, 1954, 1957)
	28	Eu	LÖVE & LÖVE (1956)
	28	Be, Ga, He, Ho, It	BRUNSBERG (1965)
	42[1]	?	HITCHCOCK & CRONQVIST (1961)
	42	Ga	BRUNSBERG (1965)
L. binatus	14	Ju	"
L. hallersteinii	14	Ju, Rm	"

In the first case the anthers were dissected out and crushed in a drop of 45 % acetic acid on a slide and were gently heated. The slides were made permanent by the plastic cover-slip method (Östergren & Heneen 1962).

According to another method after being stored in 70 % alcohol in a deep-freeze, the buds were hydrolysed in 1-N hydrocloric acid at + 60° C for 8 minutes and then, after washing in distilled water, were stained in Feulgen for 3 hours. The buds were then softened in a 2 % solution of pectinase for about half an hour and then treated in a solution of 45 % acetic acid for 10--20 minutes. The anthers were finally dissected out and crushed in the same solution and were mounted as described above.

SOMATIC CHROMOSOME NUMBERS IN THE PRESENT INVESTIGATION

The somatic chromosome numbers were counted in root tips of more than 2.000 plants from more than 500 samples of the L. pratensis complex (Appendix I, Table 2). The numbers 2n=14, 21, 28 and 42 were found in spontaneous L. pratensis (Fig. 2). Diploid L. pratensis had the widest distribution in Europe but was not found in the westernmost parts where the tetraploids mainly occured. The ranges partly overlap (Figs. 3, 4, cf. Larsen 1953, 1954, 1957). Triploids and hexaploids were found only exceptionally (Fig. 6). In L. binatus and L. hallersteinii only diploids 2n=14 were found (Figs. 2, 5).

Only exceptionally did different plants from the same collection have different chromosome numbers. In a seed sample of spontaneous L. pratensis from Paris (PPR) one plant was diploid, five tetraploid and one hexaploid. In addition many seeds did not give viable plants. The hexaploid may be the result of a fusion of an unreduced and a reduced gamete, the diploid may be a natural diploid or may have developed by parthenogenesis.

Another seed sample from the hill Lägern in the canton of Zürich in Switzerland (PSM) gave seven diploid and five tetraploid plants. A more detailed study from this area carried out by the author on material from moist meadows, woods and roadsides gave only the somatic chromosome number 2n=14 (in 45 plants from 13 populations).

Table 2. The somatic chromosome numbers of the samples of the *Lathyrus pratensis* complex studied from European countries. Aneusomaty and polysomaty are omitted.

Country	No. of samples 2n=14	2n=21	2n=28	2n=42	No. of localities seed samples	live plants
L. pratensis						
Austria	15	-	1	-	2	14
Belgium	7	-	2	-	1	8
Czechoslovakia	26	-	-	-	20	6
Denmark	29	-	-	-	1	28
Finland	10	-	-	-	7	3
France	9	2	44	1	16	38
Germany	72	-	-	-	30	42
Great Britain	-	-	19	-	14	5
Hungary	4	-	-	-	1	3
Iceland	1	-	-	-	-	1
Italy	17	-	3	-	6	14
The Netherlands	17	-	4	-	1	20
Norway	9	-	-	-	-	9
Poland	5	-	-	-	5	-
Spain	-	-	4	-	-	4
Sweden	85	1	-	-	12	74
Switzerland	41	-	6	-	5	42
USSR	8	-	-	-	7	1
Yugoslavia	46	-	2	-	10	38
L. binatus						
Yugoslavia	6	-	-	-	-	6
L. hallersteinii						
Roumania	10	-	-	-	-	10
Yugoslavia	6	-	-	-	-	6

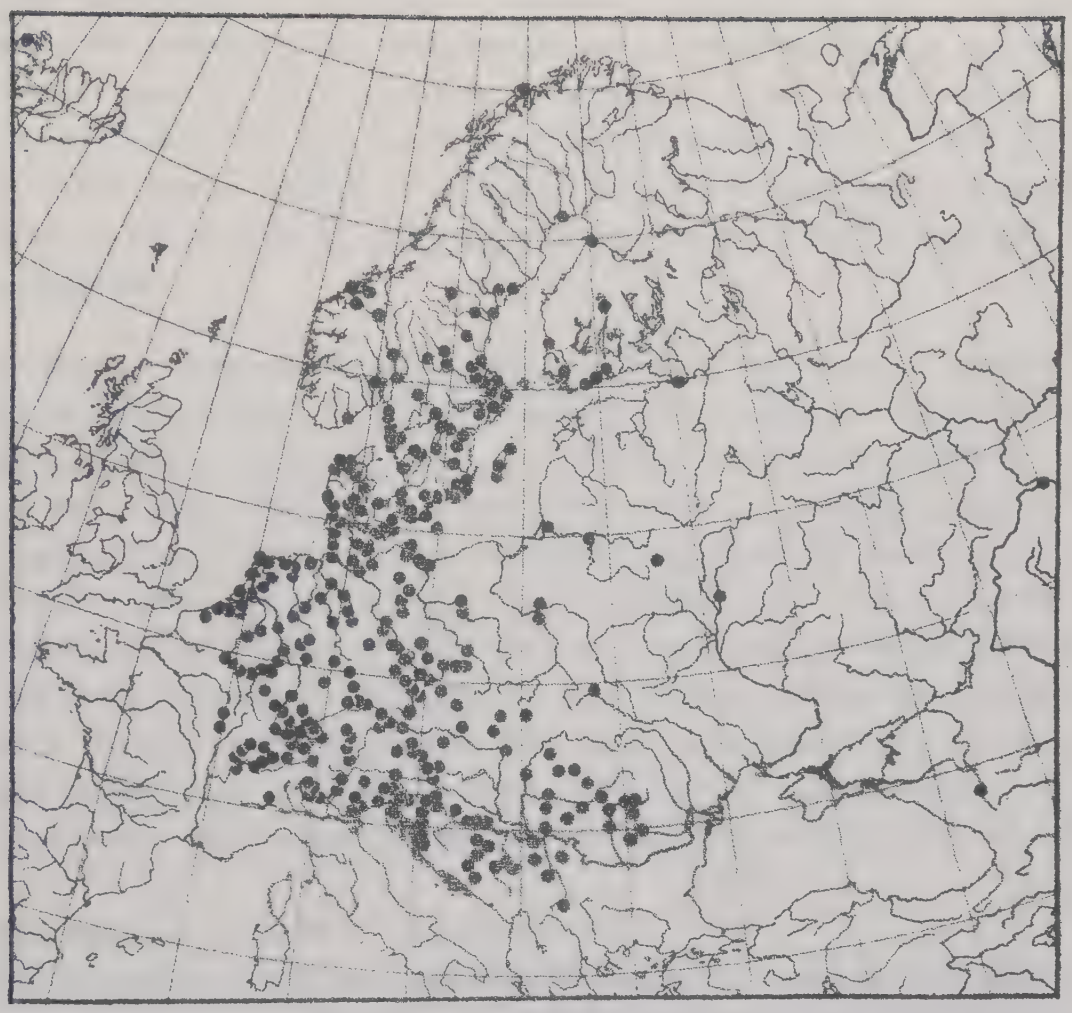


Fig. 3. Localitis of Lathyrus pratensis 2n=14, cultivated material.

One triploids collection (PCG) was observed in eastern Sweden. Probably all the triploid plants in the population belonged to one clone. Simola (1964) reported one probably triploid plant of L. pratensis from northern Finland, while the other plants of the same population were diploid. Simola questioned whether the triploid had been formed by the combination of a nonreduced and a normal reduced gamete, or by the hybridisation of a tetraploid and a diploid plant. My own experience suggests that triploids in Finland and Sweden have been formed according to the former alternative as tetraploid L. pratensis is not known to occur in these countries.

Chromosome numbers of taxa here regarded as synonyms of species of the complex may be diploid as well as tetraploid. Thus, "L. lusseri Heer" collected from its original locality Hospenthal in Switzerland (PSC) was tetraploid, while "L. pratensis var. grandiflorus Bogenhard" from the original locality Hausberg in Germany (PKU) was diploid. L. sepium Scopoli was described from Goriza in the north--eastern part of Italy. All material collected from this area was diploid. Beck (1892) reduced L. sepium to a variety of L. pratensis referring to material from Gahns and Schneeberge in Austria. Seeds from one of his herbarium specimens from Gahns germinated, and gave tetraploid plants (PTP).

ANEUSOMATY, POLYSOMATY AND ANEUPLOIDY

The phenomena of intra-individually variable chromosome numbers, aneusomaty (Duncan 1945) and polysomaty (Langlet 1927) were to a limited degree observed in the present investigation of spontaneous plants of the L. pratensis complex.

1. Aneusomaty

Aneusomaty has previously been reported from spontaneous plants mainly with vigorous vegetative propagation such as Begonia (Sharma & Bhattacharyya 1957, Meyer 1965), Hymenocallis (Snoad 1955), Artemisia maritima (Persson 1974) and various species within monocotyledonous families (Liliaceae, Amaryllidaceae, Araceae, Sharma 1956; Gramineae (Nardus), Rychlewski 1967).

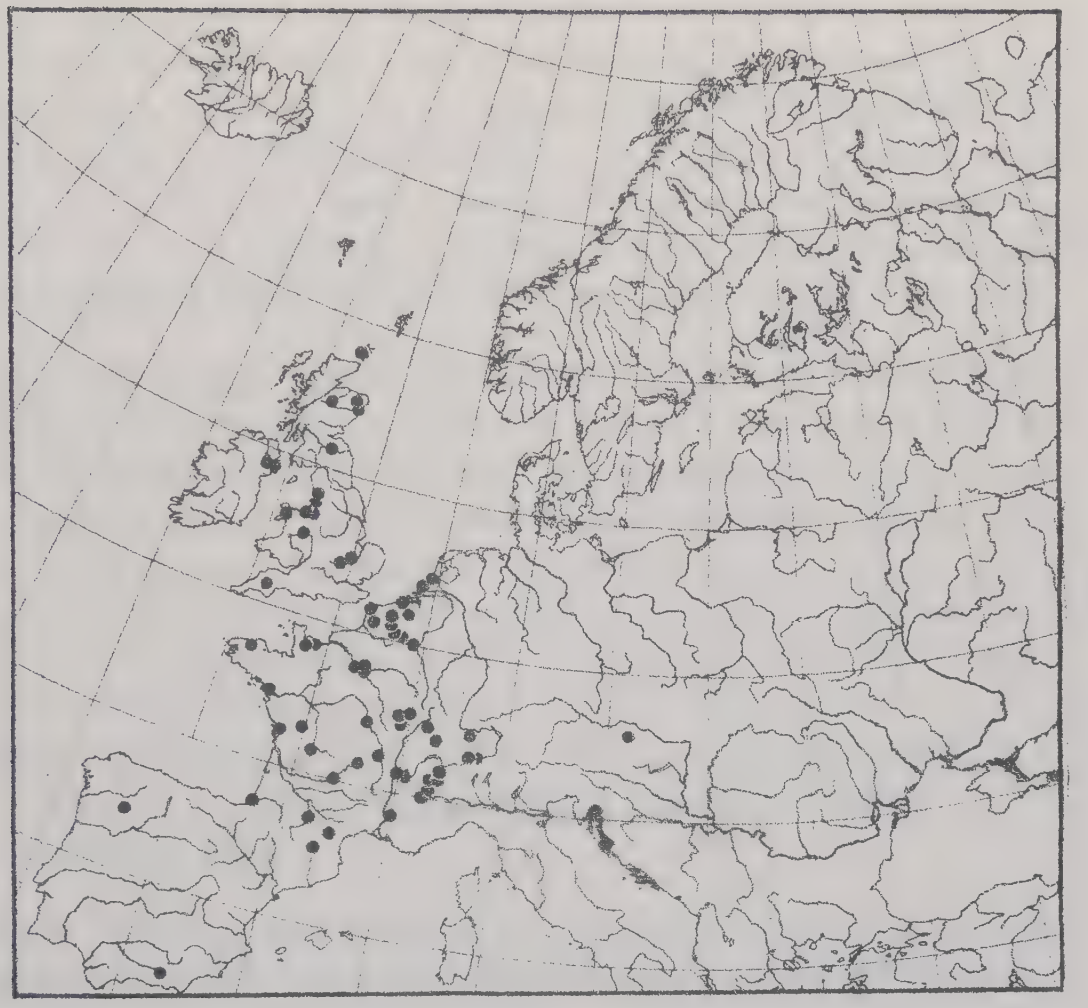


Fig. 4. Localitis of Lathyrus pratensis 2n=28, cultivated material.

In the present investigation spontaneous plants had chromosome numbers that were multiples of the basic number x=7 only. However, aneusomaty was occasionally found in sections of root tips, e. g. 2n=13, 15 or 16 in solitary cells at diploid level and the numbers 2n=24, 25, 26, 27, 30 or 38 at the tetraploid level.

The somatic chromosome numbers of about 1.800 plants of L. pratensis, 150 plants of L. hallersteinii and about 50 plants of L. binatus were counted. Normally, the somatic chromosome numbers of 7-10 cells per plant from at least three root tips were determined. In aneusomatic and polysomatic collections the somatic chromosome numbers were counted in at least 25 cells per plant.

In L. pratensis, only 11 diploid plants and 15 tetraploids were found to be aneusomatic (Table 3) which is less than 2 % of the total number of plants studied. The frequency was higher at the tetraploid level than at diploid level. The real frequency of aneusomaty may in actual fact be higher than is shown by this investigation (about 15.000 counts of the somatic chromosome numbers of about 2.000 plants). In other plants where aneusomaty has been reported the frequency is considerably higher, e. g. in Claytonia virginia 7,2 % (Lewis 1962), in Artemisia maritima 13 % (Persson 1974) and in Nardus stricta most of the plants (Rychlewski 1967).

In L. hallersteinii only one cell of about 1.000 cells counted had 2n=15 (plant NBD:28). No cells with deviating chromosome numbers were found in L. binatus. In aneusomatic diploids of L. pratensis as a rule only one chromosome was lacking or was in excess. At the tetraploid level there were often two additional chromosomes in excess or two lacking (2n=26, 30). In the present investigation no attempts were made to analyse which chromosomes were involved, but it is possible that one particular chromosome in the genome causes less genetic disturbance when present or absent in solitary cells only as in Paphiopedilum wardii (Duncan 1945).

No visible reduction in plant vitality was observed in cultivated aneusomatic plants as was found in Artemisia (Persson 1974).

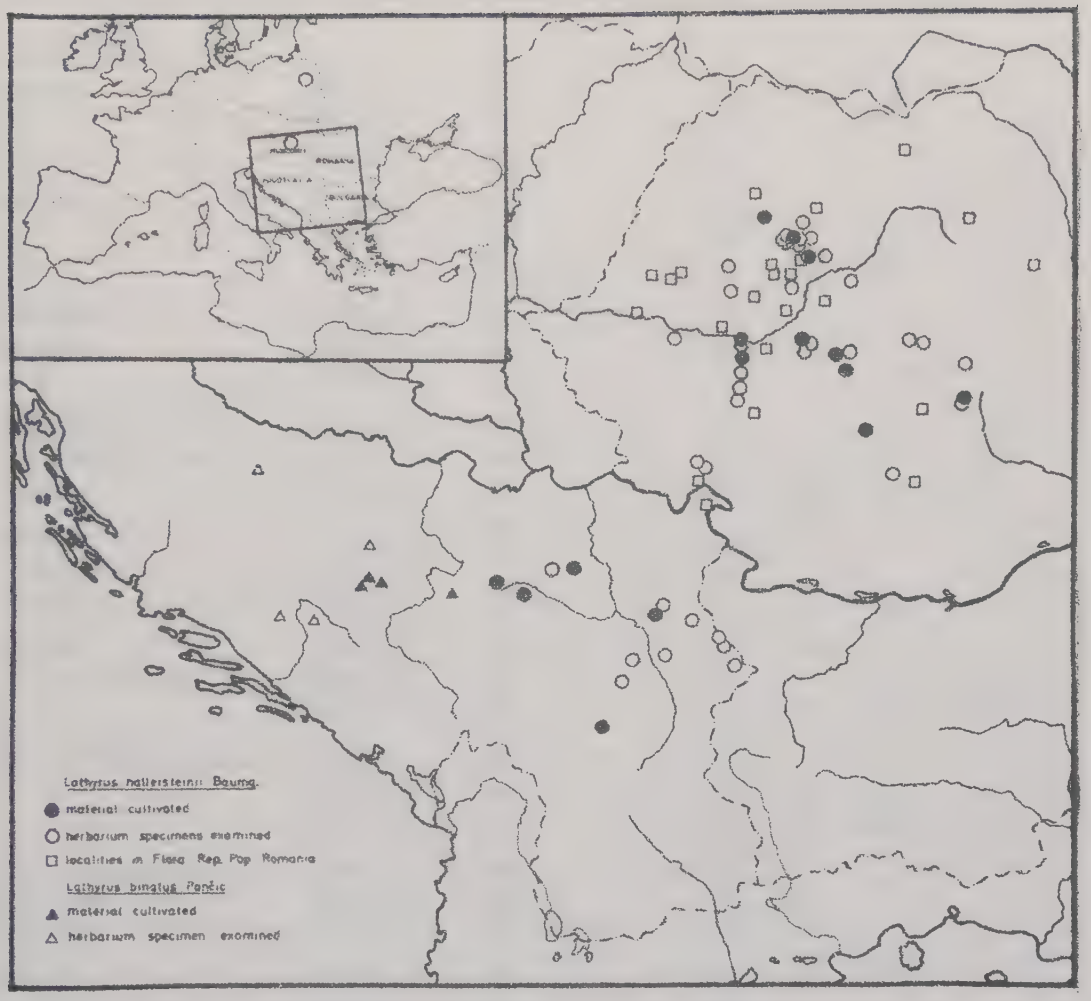


Fig. 5. Localities of Lathyrus binatus and L. hallersteinii. Cultivated material, herbarium material and localities from literature (Flora RPR, Grinţescu & Nyárády 1957).

Table 3. Aneusomatic and polysomatic plants of spontaneous *Lathyrus pratensis* and *L. hallersteinii*. [x]Plant grown from seed collected in nature. 25 counts per plant. [1]One root tip. [2]Sectional tetraploidy in one root tip.

Origin	Plant	Normal 2n	Deviating cells				
L. pratensis							
Norway	PAD:4	14	13	13	16		
"	PAB:3	14	15				
Finland	PAQ:3[x]	14	13				
Sweden	PDYT:3	14	16				
"	PCS:5	14	15				
"	PCT:4	14	15	15	16		
Sweden	PDH:2	14	15				
Denmark	PEC:4	14	21	35[1]			
"	PEV:3	14	13				
Denmark	PFA:2	14	15				
The Netherlands	PHN:3	14	15				
France	PPL:2	14	15	28[2]	26	30	
France	PPN:10[x]	14	21				
Roumania	PUB:1		21[1]				
Sweden	PCG:2	21	35				
Sweden	PCG:19	21	14				
Great Britain	PGJ:1[x]	28	25				
"	PGM:6[x]	28	25	26	27	27	27
The Netherlands	PHL:1	28	26				
"	PHL:10	28	26	30	30		
"	PHO:4	28	26	30	30	30	
The Netherlands	PHO:9	28	26				
Belgium	PJG:6	28	26	26			
France	PQYH:2[x]	28	26				
France	PPF:1	28	26	27	27		
"	PPG:2	28	27	27			
"	PQYI:2[x]	28	26				
France	PPO:4[x]	28	24	24			
"	PPT:1[x]	28	38	38			
"	PPU:1[x]	28	26				
Switzerland	PSK:3[x]	28	24	26			
Canada	PAYA:1	28	26	30	30		
L. hallersteinii							
Yugoslavia	HBE:38	14	15				

In contrast to the present study, Simola (1964) reported from Finland that aneuploid chromosome numbers often occur in L. pratensis together with the diploid ones. Presumably Simola is referring to aneusomaty. However, she added that her pretreatments of the root tips with solutions of 0,01-0,1 % colchicine, 0,002 M 8-hydroxyquinoline or a mixture of these could have produced a higher percentage of aneuploidy in her material. Simola also reported that somatic reduction was common in aneuploid cells and showed that this tendency was increased by the pretreatment. In my material as in the material studied by Simola (1964) the aberrant chromosome numbers were found in cells near the meristem of the root tips of L. pratensis.

2. Polysomaty

Polysomaty (Langlet 1927) was found in L. pratensis, too. Thus one plant from Denmark (PDC:4) had one pentaploid root tip of 12 studied and one triploid cell in a diploid root tip. In a French plant (PPN:10) and a Roumanian plant (PUB:1), both diploids, single cells were triploid. Single pentaploid or diploid cells were found in the triploid Swedish collection (PCG). In the diploid plant PPL:2 from Meuse in France the main part of one root tip was tetraploid, while a small section of it was diploid. It is possible that similar aberrant sections can arise in L. pratensis by irregular mitosis. Anomalous somatic divisions were the exception (Fig. 5, cf. Artemisia maritima, Persson 1974). The few polysomatic plants studied all showed good vitality under cultivation.

3. Aneuploidy

No aneuploids of L. pratensis were found in nature. Seeds from cultivated triploids (PCG) gave only one plant each with the chromosome numbers 2n=15, 16, 17, 19 and 26. Plants with 1-3 supernumerary chromosomes in excess showed low vitality. Such plants had poor vegetative development and reduced survival. They had e. g. a reduced number of flowers, the stem and leaflets were thickened and the leaflets often inwards curved. However, the aneuploid plants 2n=19 and 2n=26 showed good vitality and the flowering was rich, but as expected no seeds were developed.

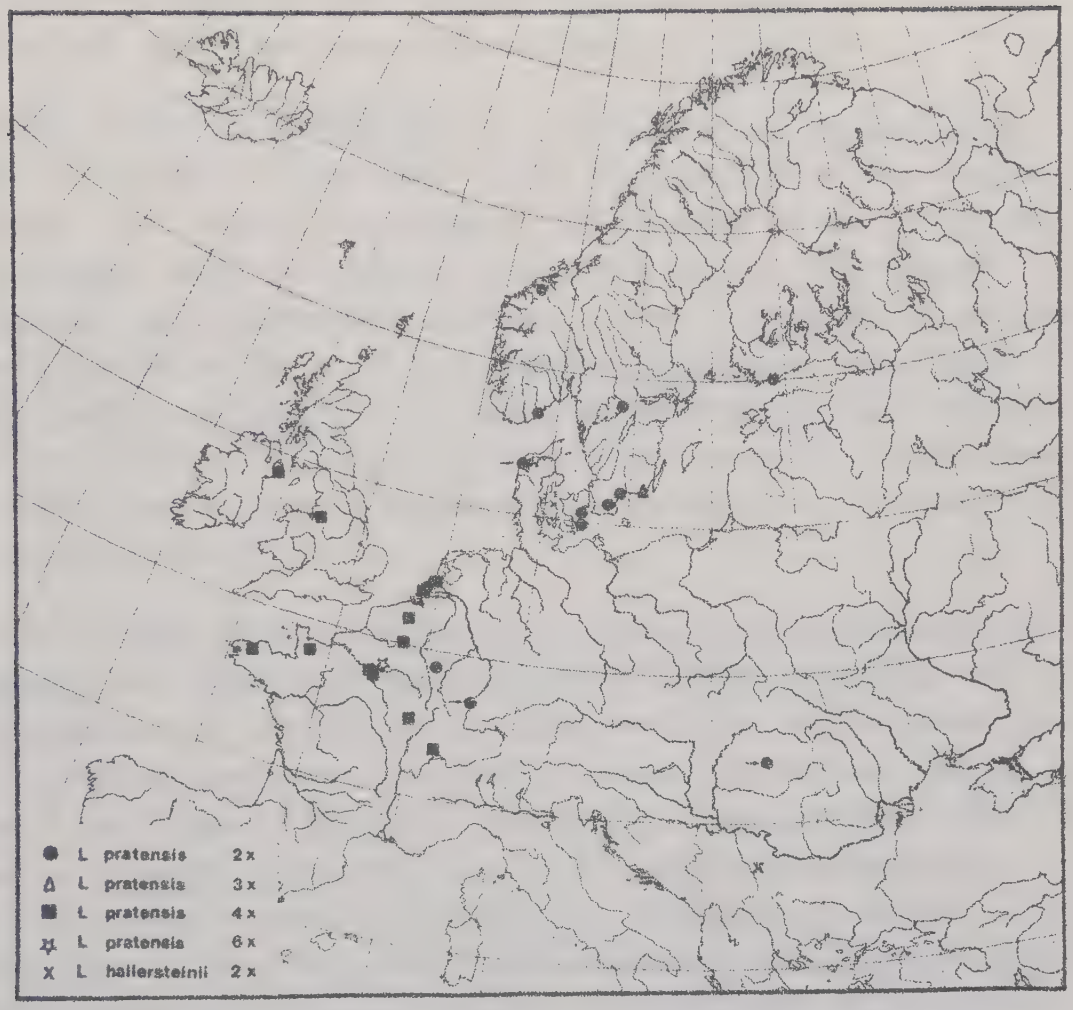


Fig. 6. Distribution of triploid and hexaploid Lathyrus pratensis and of aneusomatic and polysomatic plant samples of L. pratensis and L. hallersteinii. Arrows: polysomaty.

CHROMOSOME MORPHOLOGY

Karyotype analyses were made to a limited extent only. Thus, 7 plants from 5 populations of L. pratensis, 2 plants from different collections of L. hallersteinii and 2 plants from one population of L. binatus were studied. From each plant 5--7 measurements were made from camera lucida drawings (x 2,500).

The karyotypes of L. pratensis, L. binatus and L. hallersteinii were structurally similar and it was not possible to distinguish them in this limited investigation (cf. Bentzer et al. 1971). The chromosomes varied in length from about 4 to 8 µ. The tallest chromosome pair always had secondary constrictions. The satellites were attached to the short arm. The satellites were relatively large, about one half of the length of the short arm and of about the same size in the different taxa. Of the remaining chromosomes in the genome three were median-submedian and three ± submedian-subterminal (Fig. 8).

Relatively few detailed studies of the karyotypes of species in Lathyrus have been made (Bässler 1973). However, mutations and the phenomena of linkage and crossing over have been examined in particular in species with relatively large chromosomes (Maeda 1928, 1930, Punnet 1918, 1925, 1932, 1940, Sakamura 1920). The species of Lathyrus studied have a pair with long chromosomes with secondary constrictions as in the L. pratensis complex (Senn 1938a, Sakai 1951, Datta 1955, Favarger 1965, Wenger 1969). The remaining chromosomes are median to submedian - a karyotype configuration that has been found both in primitive and more advanced species (Bässler 1973).

MALE MEIOSIS

The aim was to compare diploid and tetraploid L. pratensis with respect to the frequency of visible meiotic irregularities and to discuss the possibility of autoploidy.

Male meiosis was studied in 15 plants from 13 populations of diploid L. pratensis and in 9 plants from 7 populations at tetraploid level. Of these, two diploid and two tetraploid

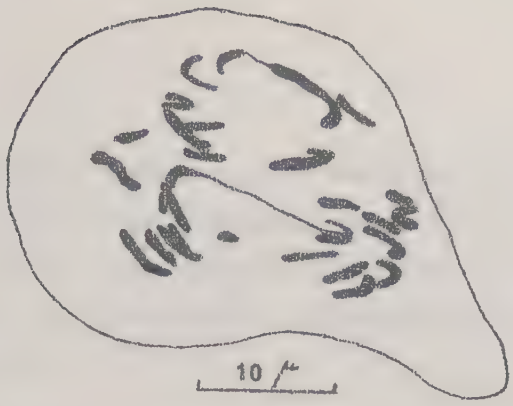


Fig. 7. Lathyrus pratensis. Disturbances in root-tip mitosis in a polysomatic plant (PEC:4).

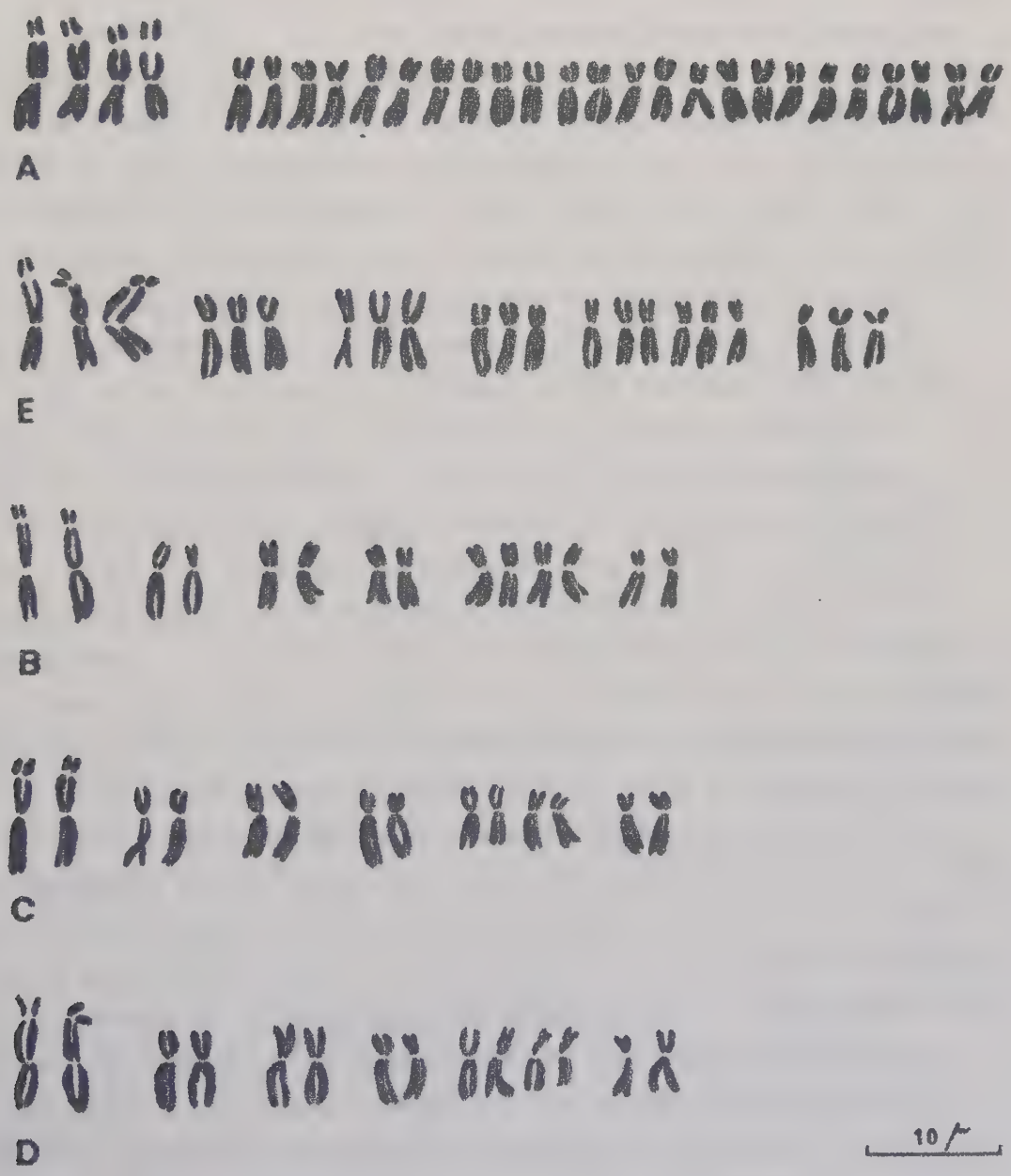


Fig. 8. Karyotypes of Lathyrus. -- A: L. pratensis 2n=28 (PPC:2). -- B: L. pratensis 2n=14 (PCF:1). -- C: L. binatus 2n=14 (BAA:1). -- D: L. hallersteinii 2n=14 (HBF:7). -- E: L. pratensis 2n=21 (PCG:11)

samples were aneusomatic. The triploid Swedish population was also investigated. Male meiosis usually took place when the buds were about 2--3 mm. long. The pollen formation is simultaneous with cell formation in a tetrahedral arrangement. The pollen grains are shed individually.

The investigations were concentrated to metaphase I and II and to anaphase I and II. In euploids of L. pratensis at diploid level meiosis at metaphase I was as a rule regular (99,7 %) with 7 bivalents formed (Fig. 9 A--D).

At tetraploid level the number of meiotic irregularities increased considerably (Table 4). Most often multivalents were formed at metaphase I -- as much as 4 quadrivalents in one single cell were counted (Table 5). The quadrivalents formed rings or were rod-shaped or more complicated in structure (Fig. 10 A, B). Besides, at metaphase I univalents were found outside the plate (Fig. 10 C). At metaphase I in euploids at tetraploid level about 45 % of the cells contained multivalents and the frequency of cells with visible chromosomal disturbances was 51,9 % in all (Table 4). As many as 44 % of the chromosomes formed multivalents in the cells studied (Table 5). Failure to pair caused lagging at anaphase I and metaphase II (Fig. 10 D). Single chromosomes could also been seen lagging outside the plate at metaphase II (Fig. 10 E). At anaphase II laggards (Fig. 10 H, I) as well as a variable number of chromosomes in the 4 nuclei (Fig. 10 F) were found. In a single cell a chromatid bridge with a fragment was found, which can be explained in several ways. It may indicate that the particular plant was heterozygous for an inversion (Fig. 10 G). Irregular second meiotic division with a tripolar spindle (cell wall formation was simultaneous) was found in tetraploid L. pratensis and it would have resulted in an unreduced cell with one diploid nucleus and two haploid nuclei instead of a normal tetrad with four haploid nuclei (Fig. 10 J), in a way similar to that reported in Solanum phureja (Höglund 1970). Relatively few cells with formation of micronuclei at the tetrad stage were found (Fig. 10 K). It is possible, but no calculation was done, that the frequency of micronuclei formation is positively correlated to the relatively low frequency of univalents lying

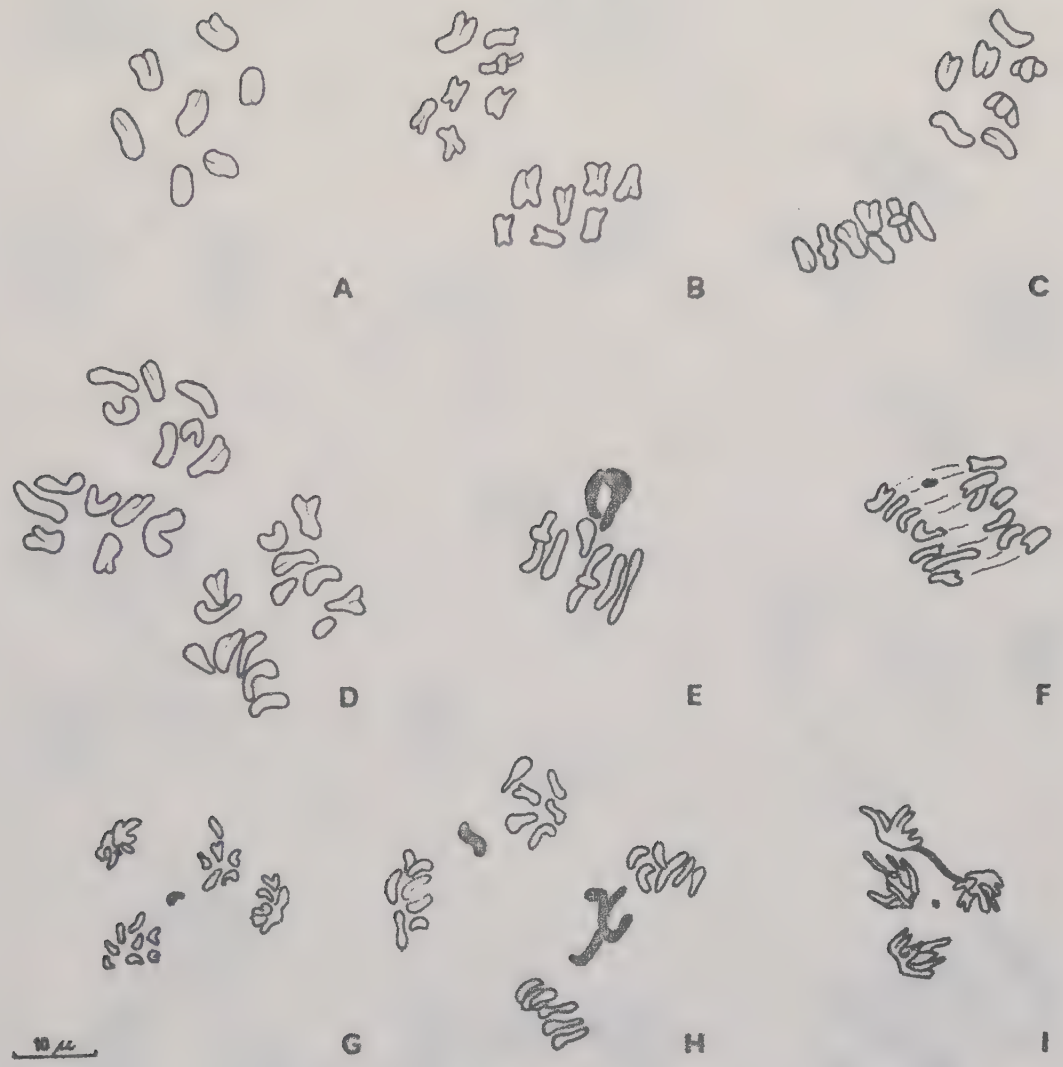


Fig. 9. Regular meiosis in Lathyrus pratensis 2n=14 (A--D) and irregular meiosis in an aneusomatic plant (E--H) and a polysomatic plant (I) of L. pratensis at diploid level. -- A: metaphase I (PMN:2). -- B: anaphase I (PHT:3). -- C: metaphase II (PED:2). -- D: anaphase II (PHY:4). -- E: metaphase I (PHN:3). -- F: anaphase I with a laggard (PHN:3). -- G: anaphase II with a laggard (PHN:3). -- H: anaphase II, bridges and a laggard (PHN:3). -- I: anaphase II - telophase II, bridge formation and lagging (PEC:4).

Fig. 10. Irregular meiosis in tetraploid Lathyrus pratensis (A — K) and in triploid L. pratensis (L). — A: metaphase I with 2 quadrivalents. (PHK:4). — B: metaphase I with 4 quadrivalents (PSH:6). — C: metaphase I with univalents (PHK:6). — D: anaphase I with a laggard (PHK:4). — E: metaphase II with a univalent (PHO:3). — F: anaphase II with a variable number of chromosomes per nucleus (PHO:3). — G: anaphase II with a bridge and a fragment (PHO:7). — H, I: anaphase II with laggards (PHO:3). — J: irregular second meiotic division with a tripolar spindle (PHO:3). — K: tetrad with a micronucleus (PHO:9). — L: metaphase I with 5 trivalents (PCG:10).

Table 4. Meiosis in *Lathyrus pratensis*. [1]Aneusomatic. [2]Polysomatic.

Coll. no.	Origin	No. of cells with normal and disturbed meiosis metaphases I and II and anaphases I and II								No. of cells studied	% cells with disturbed meiosis
		NORMAL				DISTURBED					
		MI	AI	MII	AII	MI	AI	MII	AII		
L. pratensis 2n=14											
PBM	Sweden	16	28	-	54	1	-	-	2	101	3
PDH[1]	Sweden	12	7	12	11	4	1	-	-	47	10
PED[2]	Denmark	37	-	40	14	-	-	-	1	92	1
PHJ	The Netherlands	205	-	-	-	-	-	-	-	205	0
PHN[1]	"	18	15	9	8	5	2	1	4	59	15
	"	-	-	31	62	-	-	1	-	94	1
PHP	"	-	-	65	75	-	-	-	-	140	0
PHR	"	-	-	50	96	-	-	-	-	146	0
PPJ	France	36	70	-	-	-	-	-	-	106	0
PMM	Germany	15	32	-	-	-	-	-	-	47	0
PUC	Roumania	15	-	-	38	-	-	-	-	53	0
PUP	"	22	-	-	150	-	-	-	-	172	0
PON	USSR	92	-	-	-	-	-	-	-	92	0
L. pratensis 2n=28											
PHK	The Netherlands	24	-	-	-	74	2	-	-	100	76
PHL[1]	""	3	13	-	-	7	25	-	-	48	67
PHO[1]	"	2	34	80	62	70	26	3	32	309	43
PJG	Belgium	50	56	-	25	31	5	-	-	167	22
PPB	France	25	45	-	-	8	13	-	-	91	22
PSH	Switzerland	6	27	-	9	30	10	-	4	86	51
PSD	"	-	-	-	21	-	-	-	10	31	32
PYU	Yugoslavia	37	-	-	-	10	-	-	-	47	21

Table 5. Multivalent formation at metaphase I in triploid and tetraploid *Lathyrus pratensis*. [1]Aneusomatic

Population no.	2n	No. of cells studied	No. of quadri-, tri-, bi- and univalents IV	III	II	I
PCG	21	3	0	5	2	2
"	21	4	0	4	3	3
"	21	2	0	3	4	4
"	21	1	0	3	3	6
"	21	1	0	3	2	8
"	21	1	0	2	5	5
"	21	1	0	0	7	7
"	21	1	0	0	5	11
PHO[1]	28	2	4	0	6	0
"	28	1	4	0	5	2
"	28	1	3	0	8	0
"	28	1	3	0	7	2
"	28	1	2	0	10	0
"	28	1	1	0	12	0
PSH	28	1	4	0	6	0
"	28	1	4	0	5	2
"	28	2	3	0	8	0
"	28	1	2	0	10	0
PHK	28	1	3	0	8	0
"	28	1	2	0	10	0
PJG	28	1	4	0	6	0
"	28	1	3	0	8	0

outside the plate at metaphase and negatively correlated to the frequent multivalent formation in tetraploid and triploid L. pratensis, as has been reported in e.g. Dactylis glomerata (Myers 1943), Antirrhinum majus (Sparrow, Ruttle & Nebel 1943), and Lolium perenne (Myers 1945).

Thus, at diploid level in euploids disturbances in meiosis were found only exceptionally, viz. in 0,34 % of cells examined compared with 37,7 % disturbances in meiosis, totally, at tetraploid level. The frequency of disturbances was higher in the first division of meiosis than in the second one. The greatest number of disturbances were found in tetraploid collections from the Netherlands and Switzerland.

Meiotic irregularities, such as multivalents and univalents in metaphase I and the occurrence of bridges and laggards in later stages, were found in aneusomatic plants at diploid as well as at tetraploid level (Figs. 9 E--I, 10 E--K, Table 4). The percentage of irregularities at meiosis was 16,0 % at diploid level and 45,6 % in the tetraploids of the cells studied in such plants (Table 4).

The triploid Swedish sample (PCG) showed meiotic irregularities in most cells. As many as 5 trivalents in one single cell were observed at metaphase I (Fig. 10 L, Table 5). In the cells studied 45 % of the chromosomes formed trivalents at metaphase I (Table 5) and only 30 % of the chromosomes formed bivalents.

The fact that almost all meiotic irregularities in spontaneous tetraploid and triploid L. pratensis involve the formation of multivalents is a clear criterion of autopolyploidy.

V. ISOLATION AND CROSSING EXPERIMENTS

MATERIAL AND METHODS

Only euploid plants cultivated in the open in the Botanical Gardens were used in isolation and crossing experiments. The pollen grains mature very early in the L. pratensis complex, often before the filaments stretch out from the base of the pistil. The pollen grains are, moreover, viable several days. These factors make it very difficult to emasculate the complicated papilionaceous flowers without damage. A special tubular air suction apparatus was therefore designed so whole anthers and all the pollen grains could be removed from the developed flowers without noteworthy damage. The removal of the pollen grains was checked with a binocular lins. The racemes were included in isolation bags and a few drops of water were added to get higher humidity so as to reduce flower withering. In crossing experiments the bags were opened several times to pollinate well-developed flowers only.

ISOLATION EXPERIMENTS

1. Isolation of flowers

Different species in Lathyrus have often been considered to be autogamous to a high degree. In the present study the seed formation in the L. pratensis complex was tested by isolation of the racemes in the bud stage to prevent crossings with other individuals. Isolation of the flowers, solely, gave pods in less than 4 percent of the plants of diploid and tetraploid L. pratensis (Table 6). Pods were developed in only 0,4 % of the isolated flowers. In the restricted isolation experiments with L. binatus and L. hallersteinii no pods were developed.

2. Self-pollination by mechanical treatment of stigma papillae

Pollen from the parent flower often sticks to the stigma. When flowers isolated in the bud stage were well developed, the stigma papillae were mechanically treated by drawing a dissection needle backwards and forwards in a similar way that the papillae were moved by the air suction apparatus of glass used in crossing experiments. No increase in the number of developed pods was found in this experiment (Table 7).

Table 6. Isolation experiments in the *Lathyrus pratensis* complex.

Taxa	2n	No. of isolated indiv.	No. of isolated flowers	No. of developed pods	No. of developed seeds	Pods/isol. flowers %	Seed setting no. of indiv.	Seed setting % indiv.
L. pratensis	14	337	3 375	15	25	0,4	11	3
L. pratensis	21	30	294	0	0	0	0	0
L. pratensis	28	58	836	3	5	0,4	2	4
L. binatus	14	15	36	0	0	0	0	0
L. hallersteinii	14	25	104	0	0	0	0	0

Table 7. Self-pollination in isolation by mechanical treatment of stigma papillae in the *Lathyrus pratensis* complex. Columns as above.

L. pratensis	14	154	1 605	5	10	0,3	5	3
L. pratensis	21	20	194	0	0	0	0	0
L. pratensis	28	54	453	2	3	0,4	2	4
L. binatus	14	12	16	0	0	0	0	0
L. hallersteinii	14	25	104	0	0	0	0	0

Table 8. Self-pollination in isolation by inserting pollen into the style canal in the *Lathyrus pratensis* complex.

Taxa	2n	No. of isolated indiv.	No. of isolated flowers	No. of developed pods	No. of developed seeds	Pods/isol. flowers %	Seed setting no. of indiv.	Seed setting % indiv.
L. pratensis	14	81	474	54	76	11	33	39
L. pratensis	28	21	272	28	52	10	6	29
L. binatus	14	6	12	1	1	(8)	(17)	(17)
L. hallersteinii	14	15	50	1	2	2	1	7

3. Artificial self-pollination by inserting pollen into the style canal

In isolated flowers well-developed parent pollen was inserted into the style canal with a dissection needle. By this treatment the number of developed pods in diploid and tetraploid L. pratensis was increased about ten times per individual. In relation to the number of isolated flowers the seed-setting was 30-40 times greater compared with isolation experiment 1 and 2 (Table 8). Both in L. binatus and in L. hallersteinii pods and seeds really were developed in this experiment as in contrast to the other isolation experiments. However, the material studied of this species as well as of L. binatus was very limited (cf. Davies 1957).

CROSSING EXPERIMENTS

No seed-setting has been obtained in earlier crossings between species in the L. pratensis complex or between taxa in this group and other species in Lathyrus (e. g. Melderis & Viksne 1931, Senn 1938 a, Mitchcock 1952) with the exception of the reciprocal crosses L. odoratus L. x L. pratensis (Taylor 1916). Taylor obtained one F_1 plant of grandiflora type with blue flowers in crosses with L. odoratus as mother. The reciprocal crosses gave seedlings that failed to flower. Lwin (1956) repeated such crosses but got no seeds.

1. Crosses between L. pratensis and other species in Lathyrus.

In the present study diploids (or tetraploids) of L. pratensis were crossed with European diploids (2n=14) of L. sphaericus Retz., L. maritimus Bigel., L. odoratus L., L. sylvestris L., L. latifolius L., L. heterophyllus L., L. tuberosus L., L. niger Bernh., L. montanus Bernh., L. vernus Bernh., L. venetus Rouy as well as L. palustris L. 2n=42. No hybrids were obtained in 62 crosses included 372 pollinated flowers.

Possibly, crosses of the type reported by Taylor (1916) between L. pratensis and L. odoratus might indeed have given no hybrids but maternal offspring (cf. the crossing experiments below, Lwin 1956).

Table 9. Crossing experiments with unemasculated flowers in *Lathyrus pratensis*.

Crossing combination ♀ x ♂	No. of crosses	No. of crossed flowers	No. of developed pods	No. of developed seeds	Pods/ crossed flowers %	Seed setting %
14 x 14	54	489	87	362	18	74
14 x 21	34	320	12	16	4	5
14 x 28	36	312	22	30	7	10
21 x 14	6	42	1	1	2	2
21 x 28	39	222	3	3	1	1
28 x 14	14	152	12	34	8	2
28 x 21	22	210	12	20	6	10
28 x 28	28	168	28	104	16	62

Table 10. The chromosome numbers of the offspring (F_1 plants) from the crossing experiments with emasculated flowers of *Lathyrus pratensis*. [1] One albino seedling died.

Crossing combination ♀ x ♂	No of seeds	Germination %	Number of F_1 plants 2n=14	2n=21	2n=28
14 x 14	162	92	149	0	0
14 x 21	16	56	9	0	0
14 x 28	31[1]	61	18	0	0
21 x 14	1	(100)	1	0	0
21 x 28	3	(67)	0	0	2
28 x 14	35[1]	74	0	1	25
28 x 21	20	75	0	0	15
28 x 28	105[1]	91	0	0	95

2. Crossing experiment within the L. pratensis complex with unemasculated flowers

In crosses with unemasculated flowers, in particular within taxa and ploidy levels, the seed-setting (Table 9) was much higher compared with isolatation of flowers, solely. A morphologic investigation of the offspring indicated that at least 50 percent of the F_1 plants were maternal. A few trials within L. binatus and L. hallersteinii showed similar results.

Crosses between plants of L. pratensis with different chromosome numbers gave more seeds than expected, compared with the seed-setting of isolated flowers. The seeds obtained in such crosses germinated to about 65 % and gave mainly maternal offspring (43 F_1 plants) and only one hybrid plant. A few reciproke crosses between each diploid L. pratensis, L. binatus and L. hallersteinii showed that pollen from different taxa in the complex partly stimulated selfing.

3. Crossing experiment with emasculated flowers

In crosses within taxa and ploidy level, where the flowers after emasculating were pollinated, pods were obtained in about only 20—30 % of the trials (Table 11). However, in nature the seed setting is not higher. In crosses within L. pratensis no detectable reproductive isolation between material from different geographical areas was found. Thus good seed-setting was obtained within and between diploids from e. g. Sweden, Denmark, The Netherlands, Italy and Yugoslavia and in a similar way between tetraploids from the Alps and from The Netherlands. This was also the case between different samples within L. binatus as well as within L. hallersteinii. About 80 % or more of these crosses within taxa and ploidy level gave living offspring in relation to only in a few cases between different ploidy levels, while no hybrids were received between taxa crossed in the L. pratensis complex. The crossings confirm a separation into the species L. pratensis L., L. binatus Pančić and L. hallersteinii Baumg.

Table 11. Crossing experiments with emasculated flowers in the *Lathyrus pratensis* complex.

Crossing combination ♀ x ♂	No. of crosses	No. of crossed flowers	No. of developed pods	No. of developed seeds	Pods/crossed flowers %	No. of developed plants	Germination %	Crosses with living off-spring %
prat 2n=14 x prat 2n=14	25	156	40	61	26	51	84	86
prat 2n=14 x prat 2n=21	10	48	0	0	0	0	0	0
prat 2n=14 x prat 2n=28	31	215	4	10	2	4[1]	40	7
prat 2n=14 x bin 2n=14	35	216	0	0	0	0	0	0
prat 2n=14 x hall 2n=14	29	225	2	3	1	0	0	0
prat 2n=28 x prat 2n=14	26	163	4	9	3	3	33	12
prat 2n=28 x prat 2n=21	11	59	0	0	0	0	0	0
prat 2n=28 x prat 2n=28	28	148	28	47	19	39	83	78
prat 2n=28 x bin 2n=14	12	72	0	0	0	0	0	0
prat 2n=28 x hall 2n=14	14	90	0	0	0	0	0	0
bin 2n=14 x bin 2n=14	5	16	5	11	31	9	82	100
bin 2n=14 x prat 2n=14	25	96	2	4	2	0	0	0
bin 2n=14 x prat 2n=28	5	18	0	0	0	0	0	0
bin 2n=14 x hall 2n=14	14	65	0	0	0	0	0	0
hall 2n=14 x hall 2n=14	14	95	25	41	26	30	73	93
hall 2n=14 x prat 2n=14	27	178	2	3	1	0	0	0
hall 2n=14 x prat 2n=28	5	27	0	0	0	0	0	0
hall 2n=14 x bin 2n=14	16	115	3	5	3	0	0	0

EXPERIMENT IN TRIPLOID LATHYRUS PRATENSIS

Triploids (PCG) probably clone individuals, were repeatedly placed in low temperature (shock effects) and the parent pollen was put into the style canal to get maximal seed production. From 2.720 treated flowers 26 pods with 33 seeds were obtained. The germination was 70 %. The offspring consisted of 16 diploids (2n=14) and 2 tetraploids (2n=28) and one plant each with the chromosome numbers 2n=15, 16, 17, 19 and 26.

CONCLUSIONS

The experiment showed that putting foreign pollen on the stigma favoured autogamy (cf. the uncertain occurence of spontaneous autogamy in L. pratensis according to Gams 1924). Possibly, the foreign pollen causes an enzymatic effect so the parent pollen can penetrate the stigma papillae and grow into the style canal. In nature, the flowers are pollinated by insects and the offspring may in a similar way obtained partly by autogamy and partly by allogamy. However, solitary plants of L. pratensis have all the anthers of each flower shrivelled when the stigma is developed. Thus, crossings occur in such plants and recombination and a larger variation is secured.

VI. REPRODUCTIVE BIOLOGY

FLOWERING PERIODS

L. pratensis has a wide distribution in Europe and is common in most parts, while L. binatus and L. hallersteinii only occur in southeastern parts of Europe. L. pratensis is sympatric with L. binatus and L. hallersteinii, respectively, while the two latter are allopatric (cf. Chapter VIII). Taxa in the L. pratensis complex are besides partly geographically and ecologically (cf. chapter IX) separated from each other and also isolated by partly different flowering periods.

In nature L. hallersteinii usually begins to flower in the middle of May and continues for about one month. L. binatus has about the same flowering period, mid-May to mid-June. L. pratensis begins to flower about the second week of June and often goes on for two months. In southeastern Europe, where all the three taxa studied occur, L. pratensis has a later flowering period than L. binatus and L. hallersteinii.

In cultivation L. binatus and L. hallersteinii had somewhat later flowering periods than in nature, but they flowered partly earlier than L. pratensis (Fig. 11). Cultivated diploid and tetraploid L. pratensis had about equal flowering periods (Fig. 12). However, samples from the northern parts of Europe were found to flower earlier than plants from southern Europe. Samples of both diploid and tetraploid L. pratensis from higher levels of the Alps began to flower earlier than plants from lower levels (Fig. 13). Totally, the flowering of diploid L. pratensis was more intensive during the first part of the flowering period, June - August, and at tetraploid level during the later period. The flowering period of triploid L. pratensis was June to September. Also in diploids and tetraploids the flowering periods were longer if seed-setting did not occur.

MALE FERTILITY

The male fertility was estimated by calculations of pollen stainability and pollen germination in cultivated material of

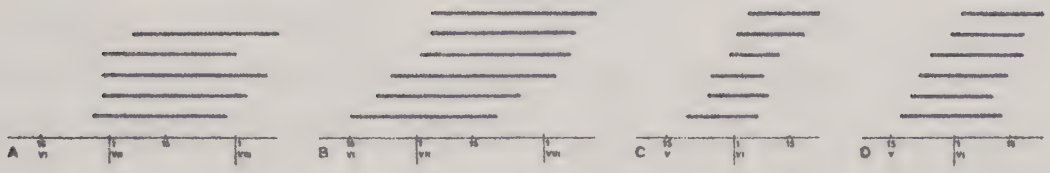


Fig. 11. Flowering period in cultivation for five (six) individuals of four Lathyrus samples. -- A: L. pratensis 2n=28 (PPF). -- B: L. pratensis 2n=14 (PAM). -- C: L. binatus (BAA). -- D: L. hallersteinii (HAF).

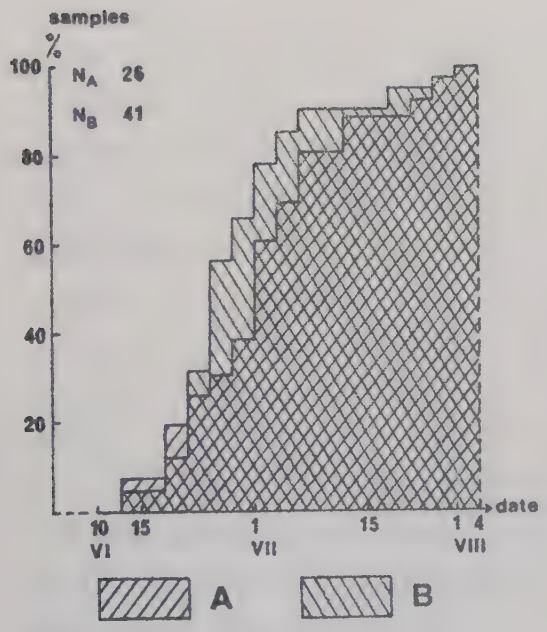


Fig. 12. Flowering period of Lathyrus pratensis in cultivation. -- A: 2n=28. -- B: 2n=14.

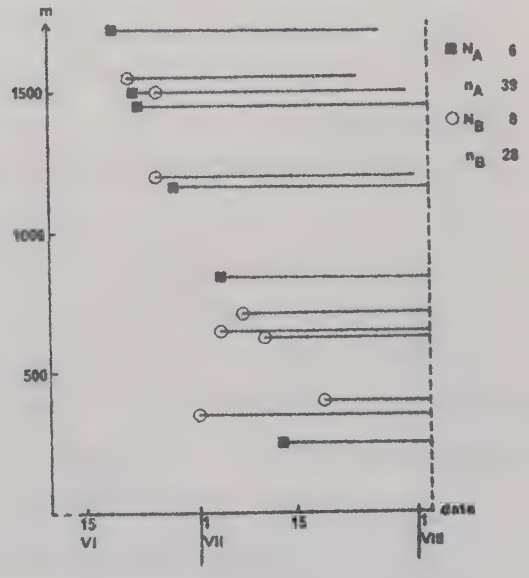


Fig. 13. Lathyrus pratensis. Commencement of flowering of cultivated material collected from different altitudes in the Alps. Filled symbols: tetraploids, unfilled symbols: diploids.

the L. pratensis complex. To get comparable results between the methods the investigation was made during the same vegetation period with the same plant material. The investigation was concentrated to diploid and tetraploid L. pratensis, but also triploid plants, probably clone individuals, and artificial tetraploids produced from triploids, were investigated. Only a few tests were made in L. hallersteinii and L. binatus.

1. Pollen stainability

Methods

Pollen grains of the L. pratensis complex were stained in lactophenol solution. About 200--300 pollen grains from each plant from 5--10 flowers were counted. Unstained, empty, often shrivelled or malformed pollen grains were classified as "bad" ones. The percentage of stained, smooth and non-vacuolised pollen grains was calculated.

Results

More than 90 percent stainable pollen grains were found in 92 % of the diploids, 60 % of the tetraploids, and 25 % of the triploids in L. pratensis (Fig. 14 A, B, E). In L. hallersteinii all the studied plants with the exception of an aneusomatic plant (HBE:28) had higher than 90 % stainable pollen (Fig. 14 D). Some plants of L. binatus had clearly reduced pollen stainability (Fig. 14 C) possibly depending on genetic disturbances in the small, isolated populations. Some plants of that taxon collected in the beginning of this century showed reduced pollen stainability, too. In the cultivated samples of L. binatus as a rule some plants in each population had good pollen stainability. However, in single flowers or whole plants in the complex unstained pollen was found occasionally.

In triploid and tetraploid L. pratensis some pollen grains were deviating from the normal sphaeroid form and were ± tetrahedral but they seemed well developed and were stainable (cf. Fig. 15 A, E, F). It is uncertain whether such pollen grains are viable as is reported in red clover and in autopolyploids in plant improvement (Eskilsson 1963).

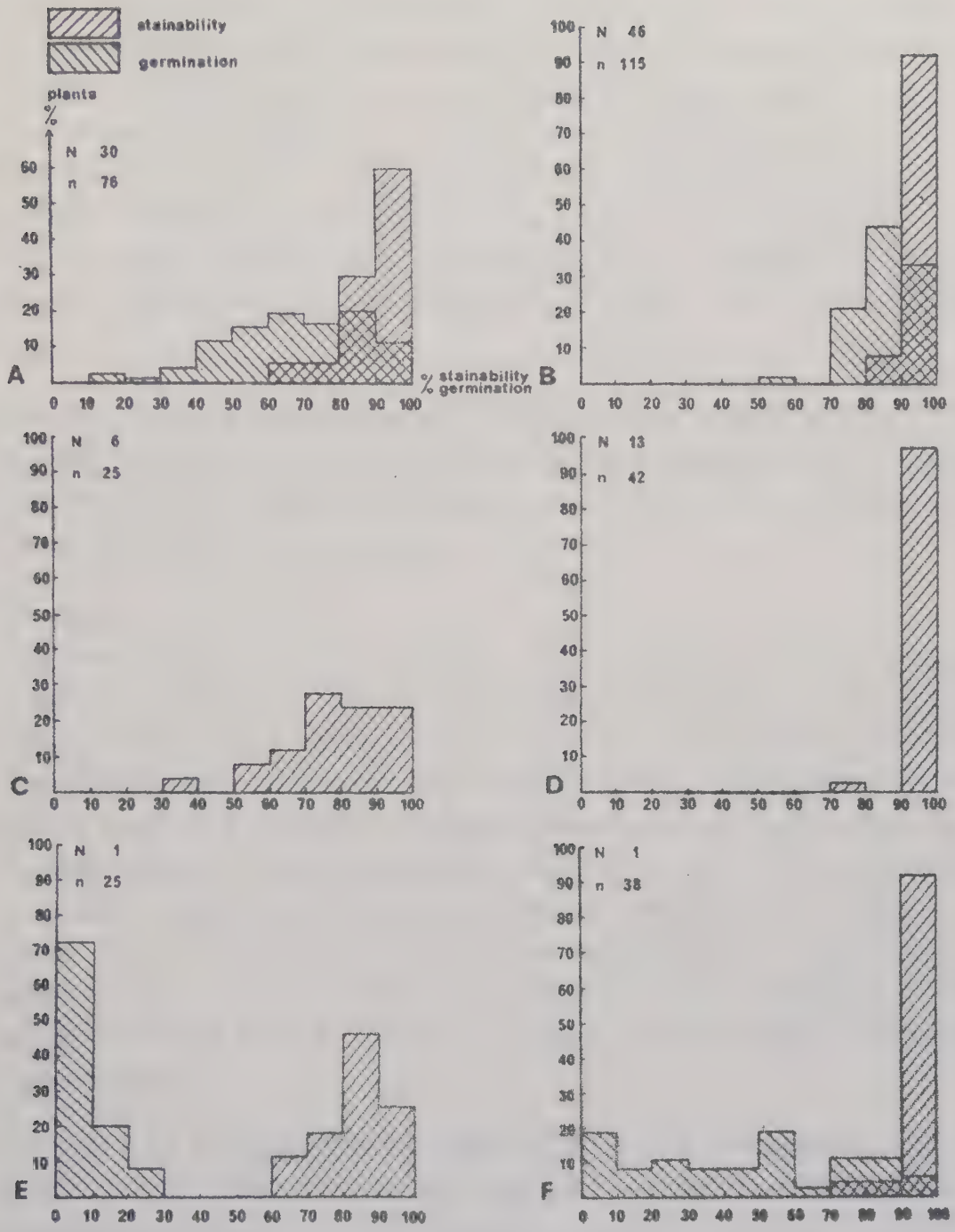


Fig. 14. Pollen stainability in cotton blue (A--F) and pollen germination on agar medium (A, B, E, F). -- A: Lathyrus pratensis 2n=28. -- B: L. pratensis 2n=14. -- C: L. binatus. -- D: L. hallersteinii. -- E: L. pratensis 2n=21. -- F: L. pratensis 2n=28, artificial.

2. Pollen germination

Methods

From living plants a small amount of pollen from 5--10 (--15) flowers was taken and spread out on fresh but hardened agar medium of varied lactose concentration in glass vessels. The following concentrations were used: 2.5, 5.0, 7.5, 10.0, 15.0 and 20.0 % lactose. A drop of water was placed on the cover before closing to get a suitable moisture. As the germination of the pollen grains began gradually and as a rule was complete after five hours, the countings were not made until the following day.

The percentages calculated are based on mean values of (4--) 5--7 (--10) trials, including different lactose concentrations, where the two lowest values are omitted. About 500--800 pollen grains from each plant were counted.

Results

For germination of the 2-nucleate pollen grains in the L. pratensis complex no definite lactose concentration was found to be optimal but it varied to a certain degree with the individuals. Generally the differences in germination between lactose concentrations was small even if a tendency to lower germination in trials with the lowest lactose concentration was found (Fig. 16). Often maximally developed pollen tubes were obtained on agar with 10 % lactose (Fig. 15). E. g. plant PSH:6 had the following mean pollen-tube lengths: 81, 91, 121, 138, 80 and 71 units after growing 5 hours on agar medium with 2.5, 5.0, 7.5, 10.0, 15.0 and 20.0 % lactose, respectively.

Totally, in L. pratensis at least 70 % pollen germination was found in more than 95 % of the diploids and only in 50 % of the tetraploids (Fig. 14 A, B). All the triploids had less than 30 % pollen germination while the artificial tetraploid offspring (2 F_1 plants) showed higher pollen germination (Fig. 14 E, F, cf. also Fig. 15 A, B, E, F).

Solitary collections of L. pratensis had lower pollen germination than normal at the respective ploidy level, e. g. a diploid collection from Czechoslovakia (PNE) had only 50--60 % pollen

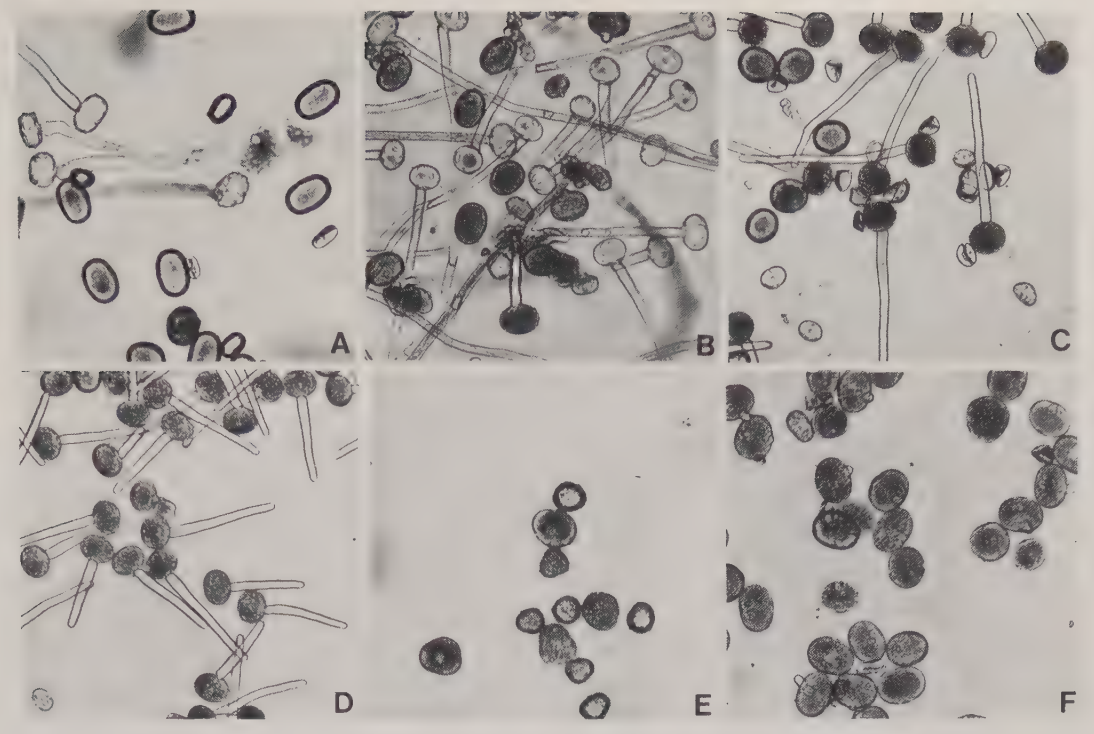


Fig. 16. Pollen germination on agar with 10% lactose after 1 hour (C–F), 6 hours (A) and 10 hours (B). Pollen grains with deviating forms occur at triploid level (E) and at tetraploid level (A, F). – A: *Lathyrus pratensis* 2n=28. – B: *L. pratensis* 2n=14. – C: *L. binatus*. – D: *L. hallersteinii*. – E: *L. pratensis* 2n=21. – F: *L. pratensis*, artificial tetraploid (2n=28).

germination although no cytological abberrations were found in this sample. One tetraploid from Belgium (PJG) that in nature was characterised by certain gigas features such as vigorous vegetative development and large flowers had 50--60 % pollen germination, while the percentage of staibale pollen was about 90 %. Both meiotic disturbances and aneusomaty were found in this collection.

The pollen germination was good in the few plants of L. hallersteinii studied (>80 %), while it was reduced in L. binatus and varied between different plants (in accordance with pollen stainability) (Fig. 15 C, D).

Discussion

In both L. pratensis and in solitary specimens of L. binatus and L. hallersteinii the percentage of germinating pollen was lower than the percentage of stainable pollen. Pollen germination trials gave better information of the probably real pollen fertility than different pollen stainability methods. The pollen germination in L. pratensis was highest at diploid level, lower in tetraploids and aneusomatic plants and as expected in the triploids. Reduced pollen fertility was found in L. binatus. L. hallersteinii had a high percentage of both stainability and germination of the pollen grains.

The investigation supports the cytological studies where plants with chromosomal abberrations really had a lower number of functionable pollen.

POLLINATION AND SEED-SETTING

Pollen taken during different stages of flower development were found to be viable (germinated on agar, cf. p. 41) for each flower about one week, sometimes longer. Pollen from the parent flower usually stuck to the stigma, so self-pollination is possible. Seed-setting was however very low in isolated racemes of cultivated material in the complex (cf. Table 6). Besides, the seed-setting of solitary individuals as well as of populations varied in different years. By artificial self-pollination (putting the parent pollen into the style canal, cf, p. 32) of cultivated

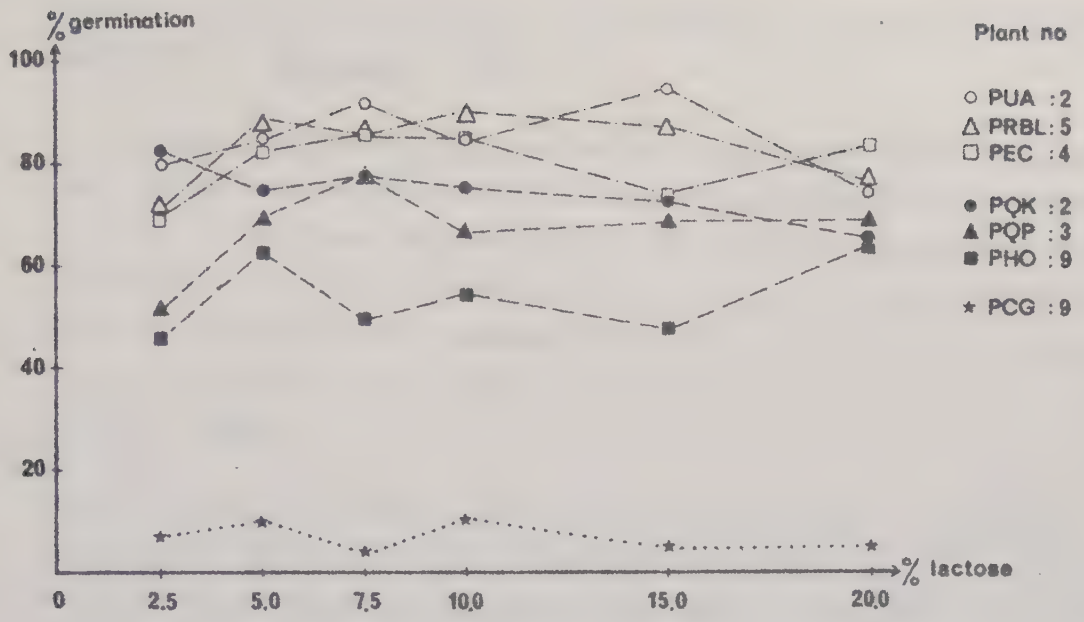


Fig. 16. Lathyrus pratensis. Pollen germination on agar with varied concentration of lactose solution. Filled symbols: tetraploids. Unfilled symbols: diploids. Star: triploid. Squares: aneusomatic plants.

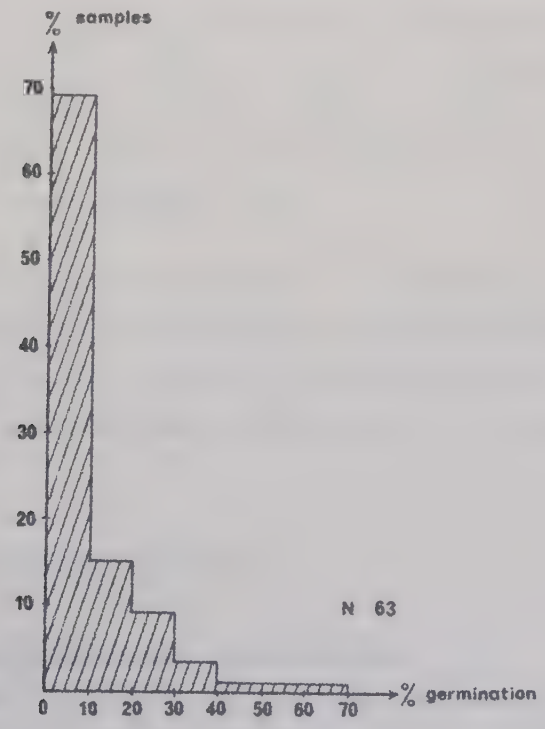


Fig. 17. Seed germination of Lathyrus pratensis. No pretreatments.

plants, the seed-setting was considerably increased at experiments mainly in L. pratensis (Table 8).

In nature, flowers are pollinated by insects and crosspollination may follow. The seed-setting (number of pods/number of flowers) of some populations checked in nature was low, usually less than 15 percent, which agrees with similar experiments of cultivated material (crosses with emasculated specimens, Table 9). Autogamy was favoured when both parent and foreign pollen grains were placed on the stigma.

The offspring of crosses with unemasculated flowers between parents at different ploidy level nearly always gave F_1 plants with the same somatic chromosome number as the mother (Table 10). In crosses with parents of L. pratensis at the same ploidy level about the half of the offspring were found maternal according to morphological comparisons with the parents. Reduced seed-setting was found in plants with irregular chromosome behaviour (triploids, aneuploids).

The results point to an incomplete barrier (that may vary in strength in different populations) to selfing within the L. pratensis complex. Probaby the barrier depends on difficulties of the parent pollen in penetrating the walls of the papillae of the stigma, while foreign pollen has the ability to do so. On the other hand the parent pollen is not blocked in its growth through the style canal; it may instead be favoured compared with individual foreign pollen tubes.

It is impossible from the present investigation to state the relative amounts of selfing and cross-fertilisation in nature. This will depend on a number of factors, both of genetic origin as well as of surrounding conditions, e. g. population structure, climate etc.

SEED GERMINATION AND DISPERSAL

1. Normal germination and periodicity

In cultivation two thirds of spontaneous seed samples of equal age of L. pratensis from different parts of Europe germinated

to only 10--15 % (Fig. 17, cf. Konold 1935-1936). The variation between different samples was high. The percentage of the seed germination during the year varied very much and was as a rule highest during the spring after a dormant period. Diploids and tetraploids behaved in the same manner. Maximal germination was obtained 6--10 weeks after sowing, sometimes later. Seeds can be kept several years and then germinate (up to 90 year old seeds from herbarium material germinated in the present investigation).

2. Germination experiments in various soil media and with different moisture

Experiments with different soil media and with different water supply gave the highest seed germination in closed germination vessels with humid papers and regular ventilation. The experiments showed that moisture is of great importance. Many seeds can be kept in soil for a very long time without visible changes such as permeability of water (swelling).

3. Germination after treatment of testa

Methods

After different pretreatments the seeds (100 seeds/sample and trial) were kept in germination vessels with humid filter and regulary ventilation for a total of five months. In all, 63 trials of each of three samples were made. In one experiment seeds were subjected to changes in temperature. Its effects on the testa were checked in order to imitate conditions in nature. The seeds were kept in water at different temperatures, -10°C, -10°C alternating with melting at 0°C on 5 occasions, 0°C, 0°C alternating 5 times with +20°, 20° and +40°C. The pretreatment periods were ½, 1, 2, 4, 8, 16 and 32 days and nights.

In another experiment the effect of 30 % sulphuric acid of the seed testa was investigated. Treatment lasted for 15, 30, 45, 60, 120, 240 or 480 minutes, respectively, at room temperature (+20°C). In one series of these experiments the seeds were pretreated in water at ±0°C for 24 hours, placed in sulphuric acid, then carefully washed and placed in germination vessels.

A third experiment investigated the permeability of the testa together with a good oxygen supply by pretreatment in 0,2 %

KNO_3 solution at +20°C for ½, 1, 2, 4, 8 or 16 days and nights.

In a fourth experiment the testa was mechanically injured by scratching with sand paper or carefully pricking with a needle so as to cause as little damage as possible.

Results

Evidently, the germination is controlled by water permeability of the testa. The highest germination, generally more than 80 % and up to 100 %, was obtained by mechanically injuring the testa, best by a needle, allowing water to penetrate; the seeds swell and germination can begin. High germination was obtained when the seeds were pretreated in -10°C and repeatedly frozen and melted or alternatively placed in +20°C for two days and nights (Table 12). There were large differences between different populations, but no general differences between diploid and tetraploid L. pratensis were found.

Table 12. Studied germination frequency of 100 seeds per sample collected in nature in the year 1962. The similar samples according to germination frequencies are listed together. Before germination the seeds were treated in a: -10° C water, b: -10° C water alternating 5 times with melting, c: 0° C water, d: 0° C water alternating 5 times with +20° C, e: +20° C water, f: +40° C water, g: 0,2 % KNO_3 solution at 20° C, h: 30 % H_2SO_4 at 20° C and, i: pretreatment in 0° C water for 24 hours and then treated in 30 % H_2SO_4.

Treatment time in days and nights	½		1		2		4		8		16		32	
	PDJ	PDC PCE	PDJ	PDC PCE	PDJ	PDC PCE	PDJ	PDC PCE	PDJ	PDC PCE	PDJ	PDC PCE	PDJ	PDC PCE
Treatment														
None	20	5												
a	64	14	48	4	52	10	32	16	60	12	60	6	40	10
b	52	6	100	14	72	20	72	8	56	8	16	6	20	6
c	32	10	64	6	36	8	28	14	34	7	50	2	36	4
d	40	6	84	8	60	4	44	4	52	10	72	4	12	5
e	48	14	56	4	88	20	60	14	64	10	16	4	8	8
f	52	16	28	10	28	4	8	8	0	0	0	6	0	4
g	80	6	72	8	68	12	44	12	80	14	40	36	-	-

Minutes of treatment	15		30		45		60		120		240		480	
	PDJ	PDC PCE	PDJ	PDC PCE	PDJ	PDC PCE	PDJ	PDC PCE	PDJ	PDC PCE	PDJ	PDC PCE	PDJ	PDC PCE
Treatment														
h	48	8	51	10	48	8	44	6	32	4	25	3	20	0

4. Dispersal

Taxa in the L. pratensis complex are essentially spread by means of single seeds. They have no adherence ability, and no autochorous mechanism is developed. The seeds are rather heavy and are not dispersed widely by themselves.

By man that occasionally carry or transport the plants e. g. of hay and by animals (that eat the plants) seeds may by spread long distances. The seeds may pass through the intestines of the animals and still germinate (cf. Table 12). As L. pratensis sometimes grows on seashores (the epilittoral zone) as well as on riverbanks the seeds, which to a certain extent can float, may be dispersed by water and then have the ability to germinate (cf. Table 12). L. binatus grows on scree slopes, so the seeds can easily be spread to lower situated localities. L. hallersteinii often grows in woodlands with Quercus or Fagus and both its dispersal and colonisation may be favoured by animals that feed on and trample the ground (e. g. sheep, swine).

ASEXUAL REPRODUCTION

Vegetative proliferation occurs by horisontal rhizomes. Material of the L. pratensis complex in cultivation showed no notable differences between the studied taxa. Up to 7 m long rhizomes were developed during one vegetation period.

In nature, rhizomes were found in all the studied taxa of the complex. They were more conspicious in L. pratensis but are also well developed in L. binatus. In L. hallersteinii they were fewer in number than in other taxa. However, in nature the variation between individuals and populations was very wide and evidently highly influenced by the surroundings. Survival and vigorous vegetative development (about 100 m^2) of the triploid population studied were found during 15 years.

VII. ARTIFICIAL POLYPLOIDS

To obtain plants of L. pratensis with the double chromosome number, a large number of recently germinated seeds from diploids with about 1--2 mm. of the root showing were treated in 0.063, 0.125, 0.250, 0.500 and 1.000 % colchicine solution for various times up to 4 hours. Most tetraploid plants were obtained when such seeds were placed in 0.125 % colchicine solution for 2--3 hours before germination (cf. in Vicia, Nordenskiöld 1953). Most plants had partly tetraploid and partly diploid shoots and roots and often gradually reverted to the diploid level.

In another trial the triploid Swedish population (POG) was used. This had probably arisen by fusion of an nonreduced and a reduced gamet from diploid L. pratensis (cf. p. 15). After comprehensive trials to get offspring from the triploids, among others two tetraploids were obtained.

These tetraploids can be considered as autotetraploids owing to the origin e.g. geographic of the parent triploid and the relatively high trivalent formation in its meiosis (cf. p.29, Table 5). The artificial tetraploids also showed disturbances in meiosis with multivalent formation in metaphase I and bridges in anaphase I and II.

The pollen stainability (Fig. 14:F) was high in the artificial tetraploids compared with the triploids (Fig. 14:E), while the pollen germination was reduced. It varied greatly in these tetraploids but was as expected higher depending on more balanced chromosomal behaviour than in the parental triploid. Pollen germination was lower than in the spontaneous tetraploids (Fig.14 A,F). By selection, the frequency of balanced gametes will probably be higher in the following generations.

The artificial tetraploids were morphologically equal to the parental triploid. However, during the first two years in cultivation, at least, they had less vegetative development than the triploid plants. The leaves and the stipules were somewhat larger in the artificial tetraploids as well as in spontaneous

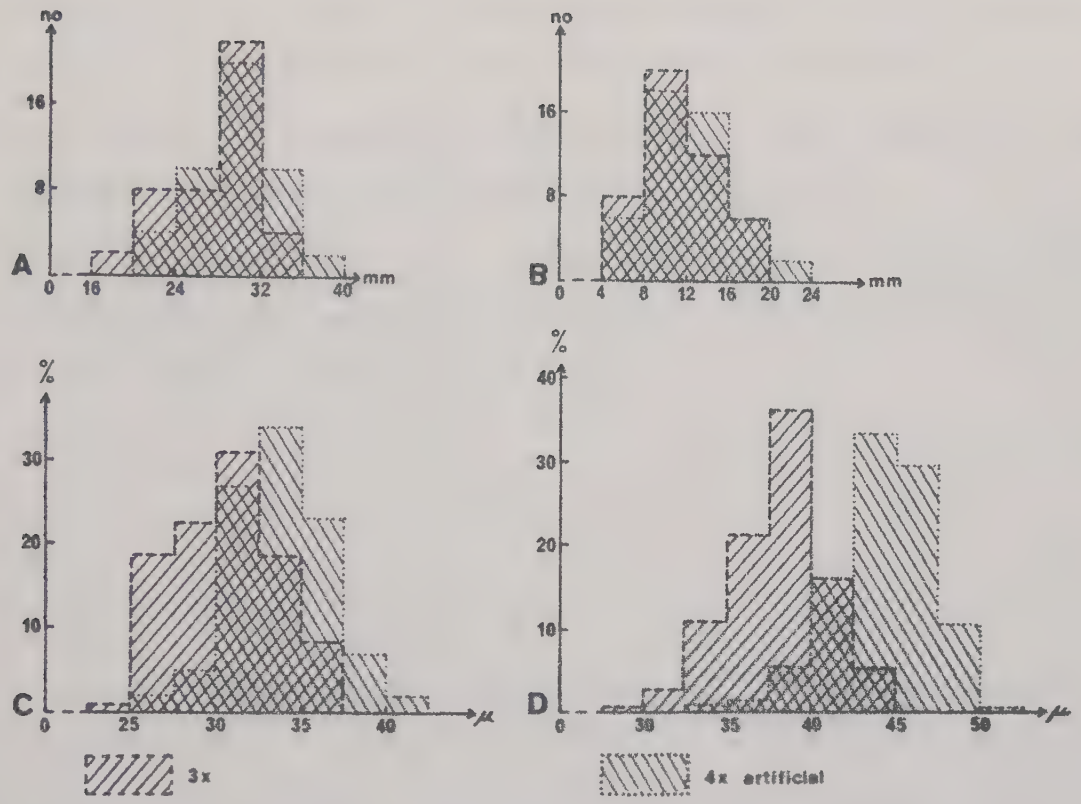


Fig. 18. Triploid (3x) and artificial tetraploid (4x) Lathyrus pratensis. -- A: Length of leaflets. -- B: Lengths of stipules. -- C: Stomata length. -- D: Largest pollen diameter. -- A, B: Means of 2--4 measurements per plant. -- C, D: Means of at least 10 measurements per plant.

tetraploids than in the triploids (Fig. 18 A, B). The stomata of the artificial tetraploids were somewhat larger than those of the spontaneous tetraploids and were generally larger at tetraploid level than at triploid level (Fig. 18 C). The variation of the size of the pollen grains of the artificial tetraploids was within the variation of the spontaneous material (Fig. 18 D). Considerable differences in size occured between the parental triploid and the artificial tetraploids. In cultivation the number of developed flowers of the produced tetraploids was smaller than at triploid level and at tetraploid level of spontaneous material.

The artificial tetraploids began to flower late, while the triploids flowered for about three months (June--September).

A few crosses between the artificial tetraploids and spontaneous tetraploids gave seeds that germinated in crosses with spontaneous plants from the Alps (FVI) as mother.

VIII. GEOGRAPHIC DISTRIBUTION

LATHYRUS PRATENSIS

L. pratensis is considered to be spontaneous in Europe and Asia (Alefeld 1861) and northern Africa (Fig. 19) but introduced and rare in North (Fig. 20) and South America (White 1894, Hitchcock 1952, Hultén 1958, Hitchcock & Cronqvist 1961, Burkart 1935). L. pratensis was referred to the group West-European-Middle-Siberian plants by Hultén (1971).

In Asia (Fig. 21) L. pratensis is reported from the whole of West Sibiria, Central Sibiria viz. Aral, Pribahl, Tjan-Sehan (Korobin 1955), East Sibiria viz. Jenisei, Ang. Sajan, Davurien, (Komarov 1948, 1950, 1951), Japan, China, Mongolia, West Himalayas, Iran, Kaukasus (Kavjatin 1954), Turkistan, Armenia, Syria (Post 1932--1933) and Asia Minor (Davis 1970).

From Africa L. pratensis is mentioned from areas at high altitudes in Morocco and Abyssinia.

In Europe L. pratensis is usually common (Crantz 1769, De Candolle 1825, Gams 1924, Grinţescu & Nyárády 1957, Koch 1843, 1845, Marchesetti 1896--97, Reichenbach 1830--32, Reichenbach & Beck de Mannagetta 1903, Rouy 1899, Schinz & Keller 1905, cf. Figs. 3, 4) with diminished frequence in the southern (Fig. 22) and northern parts. L. pratensis is reported from Portugal, Spain (Picot de Lapeyrouse 1818, Willkomm & Lange 1880), Italy and Corsica (Marchesetti 1896--1897, Arcangeli 1884) and Greece (Rechinger 1943) as well as from Iceland, Norway, Sweden, Finland and Russia (Hultén 1971: Fig. 1171, Löve & Löve 1956, 1961. L. pratensis is considered recently to occur in higher frequency or to have been spread in the northern parts of Finland (Simola 1964), Norway (Vorren 1968) and the Faeroes (Hansen 1966).

Field studies in Europe showed that L. pratensis grows from sea level up to 2.200 m in the western part of the Alps. In mountain areas L. pratensis often grows a few hundred meters above the tree line.

Fig. 19. Distribution of the Lathyrus pratensis complex. Introduced L. pratensis in North America (see fig. 20).

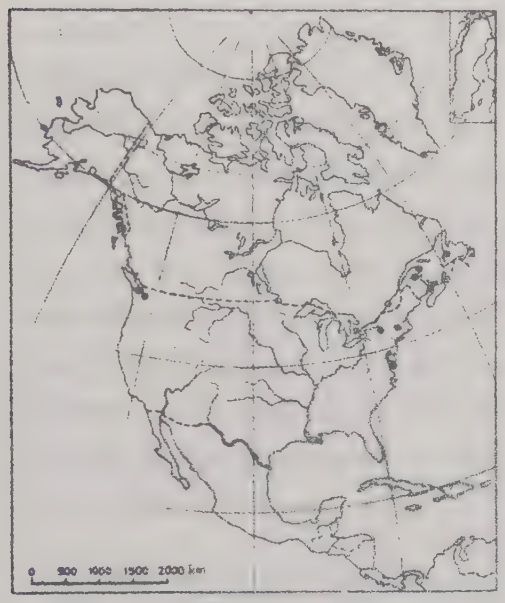


Fig. 20. Distribution of Lathyrus pratensis in North America according to controlled herbarium material.

Fig. 21. Distribution of Lathyrus pratensis in Asia and European Russia according to controlled herbarium material.

Fig. 22. Distribution of Lathyrus pratensis in Portugal, Spain, Italy south of the river Po, the southern parts of Yugoslavia, Albania, Bulgaria and Greece according to controlled herbarium

L. lusseri Heer that was reported from the Alps, particularly from the southern parts (original locality Hospenthal (Uri) in Switzerland, cf. cultivated PSG) with synonyms described from France and Germany is here included in L. pratensis (cf. p. 15). In the same manner L. sepium Scop. that was described from cultivated areas around Goriza in the north-eastern part of Italy is included in L. pratensis.

Morphologically, it was not possible to distinguish herbarium material of L. pratensis at different ploidy levels. From cultivated samples it is evident that the diploids had the widest distribution in Europe (Fig. 3), while the tetraploids were found in the westernmost parts. In Great Britain only tetraploids have been found (Fig. 4, Marks 1950, Larsen 1957). In a zone through the Netherlands, Belgium and France there were both diploids and tetraploids. In the Alps (France, Switzerland and Italy) the tetraploids were commonly found at high altitudes (above 1.200 m), while the diploids occured mainly at lower levels. Tetraploids were seldom found in Austria and Yugoslavia (cf. Fig. 4, Appendix I).

Only one triploid population was observed in this investigation, namely in the province of Blekinge, Sweden (PCG) (Fig. 6). One triploid plant is also reported from the north part of Finland, from Hyrynsalmi (Simola 1964). At hexaploid level of L. pratensis one spontaneous French plant (PPR:2, Fig. 6) and one plant from the Botanical Gardens in Leopolis (Lemberg), Austria were found in this investigation.

LATHYRUS BINATUS

L. binatus has a very limited distribution and is only reported from Yugoslavia, in the western part of Serbia and in Bosna and Hercegovina (Fig. 5). Of all herbaria material revised only 32 sheets of L. binatus were found (Appendix 2).

LATHYRUS HALLERSTEINII

L. hallersteinii is mainly distributed in Roumania and Yugoslavia (Grinţescu & Nyárády 1957, Hayek 1924--1927). One sheet from Poland, from Bug, Zajeczniki at Loise in the district of Warszawa, collected by Kars in 1873 and kept in Florence was found as well as one sheet from Hungary, Pest, Osca, Müller 1856. In literature L. hallersteinii is not mentioned from Poland, Hungary or Austria (e.g. Szatera 1959, Soó 1966,Neilreich 1859, 1866). Ball 1968 in Flora Europaea reported L. hallersteinii from Greece. The species is not mentioned from the neighbouring Bulgaria (Stojanoff & Stefanoff 1933). Comprehensive herbarium investigations (about 200 sheets of L. hallersteinii were found, Appendix II) together with literature studies and several excursions to collect living plants in large parts of Europe confirm that the distribution of L. hallersteinii is probably almost limited to Roumania and Serbia in Yugoslavia (Fig. 5). In this investigation L. hallersteinii was found in the field about one hundred kilometres further west than had been known earlier.

CONCLUSION

From what we know at present L. binatus and L. hallersteinii are allopatric species; in south-eastern Europe they were found to be separated from each other by a distance of only about 30 kilometres. L. pratensis, which is common in nearly all of Europe, although more rare in the most southern and northern parts, occurs in the same geographical areas as L. binatus and L. hallersteinii, respectively (sympatric species).

IX. THE OCCURENCE OF THE LATHYRUS PRATENSIS COMPLEX IN DIFFERENT PLANT COMMUNITIES

"Lathyrus pratensis kann beinahe als Rasenubiquist gelten, wenn er auch die trockensten Wiesentypen, die alpinen Wiesen und die stärker sauren Humusböden meidet" (Gams 1924).

MATERIAL AND METHODS

In the field the characteristic species of the plant community were usually noted in each locality where plants of the Lathyrus pratensis complex were sampled. Below, the wide ecological occurence of L. pratensis in Europe is presented by some examples of plant communities where the species is reported in literature or was found in this investigation. The nomenclature used is mainly after Tutin et al. (1964--1972) and Hylander (1955).

In the southeastern parts of Europe, where L. pratensis, L. binatus and L. hallersteinii all occur, some selected sample areas were analysed in more detail to exemplify the floristic composition. From each locality studied 15 standard areas, each 1 m^2, were floristically studied. The degree of cover was estimated with a five-degree scale of Hult, Sernander & Du Rietz (Du Rietz 1921), extended with a lowest degreee ($x \leq 1$ % cover). The primary data are summarised in a survey-frequency table. In the table standard area frequencies (number of standard areas where the species was found, calculated as a percentage of total number of standard areas) are given for the 8 localities studied. The characteristic degreee of cover is calculated according to Malmer (1962, p. 49) and placed as the exponent of the frequency figure (F^c).

From 39 localities of species of the Lathyrus pratensis complex some chemical properties of dried soils from a level of 5--10 cm. were determined. The material sampled during five weeks in May--June 1965 was first air-dried and then heated to constant weight at ca 105° C. Exchangeable metallic cations and hydrogen ions were extracted with 1 M ammonium acetate (NH_4Ac) of pH 7.00 in an equilibrium extraction. 14 g dried sample of fine

earth was shaken in a polythene bottle with 140 ml 1 M NH_4Ac on a rotating board for eight hours and then filtered. The exchangeable hydrogen ions were determined as the pH difference between pure extractant and soil filtrate, converted into hydrogen concentration using the titration curve of the pure extractant. An aliquot of the pure filtrate was evaporated to dryness and digested with HNO_3 + $HClO_4$ (4:1). The clear digest was reevaporated to dryness and the residue dissolved in 0.1 HCl.

p H was determined electrometrically with separate glass and reference electrodes (pH-meter type Radiometer) in extracts of water and 0.2 M KCl. S o d i u m and p o t a s s i u m were determined flame-photometrically, c a l c i u m and m a g n e s i u m by titration with Na-EDTA according to Schwarzenbach (1957). M a n g a n e s e was determined colorimetrically with potassium periodate (KIO_4) according to Sandell 1944, p h o s p h a t e colorimetrically by the "Molybdate" method (modification of method described by Jackson 1958, cf. Tyler 1967). The extractant used was 1 M HAc. L o s s o n i g n i t i o n (an approximate estimation of organic matter) was determined by ignition at ca. 550° C in a muffle furnace.

PLANT COMMUNITIES WITH LATHYRUS PRATENSIS

Oberdorfer (1957), in his collation of plant communities from the southern part of Germany includes L. pratensis in the association Arctietum nemorosi of the Atropion and in the Salici-Pinetum of the Erico-Pinion.

L. pratensis is most common within the Molinietalia (Oberdorfer 1957), where it occurs in the following associations: Trollio-Juncetum, Crepido-Juncetum acutiflori, Polygono-Scirpetum, Filiformi-Scirpetum, Polygono-Brometum, Cirsio-Polygonetum, Trollio-Cirsietum, Filipendulo-Geranietum, Molinietum medioeuropaeum, Asclepiado-Molinietum and Scorzonero-Molinietum. Within Arrhenatheretalia L. pratensis occurs in the following associations: Arrhenatheretum medioeuropaeum, Centaureo nigrae-Arrhenatheretum, Poa-Trisetetum, Melandrio-Arrhenatheretum, Astrantio-Trisetum and Meo-Festucetum.

L. pratensis in tall-herb meadow vegetation

L. pratensis was found in tall-herb meadows characterised by e.g.: Circium oleraceum, C. palustre, Filipendula ulmaria, Galium palustre, Lotus corniculatus, Lychnis flos cuculi, Mentha arvensis, R. repens, Thalictrum flavum, Valeriana officinalis, Poa pratensis, A. stolonifera, Festuca pratensis, F. rubra, Poa trivialis and Holcus lanatus. In such plant communities of the northern parts of Europe L. pratensis and L. palustris sometimes exist together (e. g. PEC, PBK). No crossings between these two species were found in these localities.

A vegetation similar to the Trollio-Cirsietum of the Molinetalia according to Oberdorfer's classification (1957) was relatively common, e.g. in subalpine meadows in the Alps. In e. g. Rotherthurm, Switzerland, 850 m above sealevel (PRK), L. pratensis grew together with Chrysantemum leucanthemum, Circum oleraceum, C. palustre, Crepis paludosa, Dactylorchis maculata, Filipendula ulmaria, Gentiana lutea, Gymnadenia conopsea, Lotus corniculatus, Lychnis flos cuculi, Polygonum bistorta, Ranunculus acris, R. repens, Sanguisorba officinalis, Trollius europaeus, Valeriana dioca, Veratrum album, Vicia cracca, Alopecurus pratensis, Anthoxanthum odoratum, Briza media, Carex disticha, C. nigra, C. panicea, Cyrosurus cristatus, Festuca rubra, F. pratensis, Holcus lanatus, Molinia caerulea, Poa pratensis (Fig. 23, cf. Brunsberg 1974, p. 37: PDYN, p. 39: PDYK, p. 43: PDYM, p. 45: PDYL).

In such tall-herb meadows diploid L. pratensis (e. g. PRG, PRK, PRY) as well as tetraploids (e.g. PSG) were found. In this investigation no differences were found in the species composition of the tall-herb meadow between different ploidy levels of L. pratensis.

L. pratensis in vegetation of shores, banks and roadsides

Transitions from wet to ± dry conditions were found in the vegetation of shores, banks and roadsides, where L. pratensis often occurs. The plant communities in such localities are often composed of the same species as in the tall-herb vegetation but

Fig. 23. Top: Subalpine meadow in the Alps with *Lathyrus pratensis* in closed vegetation. Switzerland, Rotenthurm, 850 m (PRK). Photo: author, July 1963. – Bottom: Oakwood with well-developed shrub layer (right: detail) with *Lathyrus hallersteinii* (in frame). Yugoslavia, Kragujevac, 450 m (HBC). Photo: author, May 1965.

Fig. 24. Calcareous scree slope with *Lathyrus binatus* (bottom: detail). Yugoslavia, Sarajevo, 950 m (BAA). Photo: author, May 1965.

commonly some species are lacking. Others are found, e.g. Phragmites communis, Dactylis glomerata, Anthriscus silvestris and Pastinaca sativa. Often L. pratensis occurs on banks of small streams, rivers and canals and on roadsides in most parts of Europe. Certainly, L. pratensis prefers localities with a good supply of light to sites in the shade. The soil where L. pratensis grows can be a clay, mould or sand and mixtures of them, sometimes with intermixture of stones.

On a slope with chalk and a good ground water supply near the beach on Mön, Denmark, where Equisetum telmateia dominated, diploid L. pratensis (PFA) were found together with e.g. Dactylordhis maculata, Origanum vulgare and Brachypodium sylvaticum.

At the Baltic Sea, L. pratensis occurs in the tall-herb meadow in the epilittoral zone (according to the littoral terminology of Du Rietz 1950), e.g. in the southeast part of Sweden (Brunsberg 1969, p. 141). It is recorded in the Deschampsia caespitosa community as well as in the Agrostis tenuis - Festuca ovina community of the epilittoral meadow vegetation in the eastern parts of Sweden (Tyler 1969, p. 83). At the Baltic Sea L. pratensis sometimes grows among stones near the water, too.

On shores of lakes e.g. in Sweden L. pratensis is often found in the upper zone of tall-herb vegetation, namely in the Filipenduala ulmaria - Deschampsia caespitosa community as well as in the Festuca - Agrostis tenuis community, e.g. on the shore of Lake Båven, Sweden, according to a belt-transect analysis (cf also Brunsberg 1972, p. 37).

L. pratensis in dry-meadow vegetation

L. pratensis was less often found in dry-meadow vegetation, e.g. in Marville, France (PPL), together with, e.g., Achillea millefolium Centaurea scabiosa, Daucus carota, Galium boreale, G. verum, Hieracium umbellatum, Hypericum perforatum, Knautia arvensis, Origanum vulgare, Pimpinella saxifraga, Potentilla erecta, Ranunculus acris, Rhinanthus major, Sanguisorba minor,

Vicia cracca, and the grasses: Agrostis tenuis, Arrhenatherum elatior, Cynosurus cristatus, Festuca pratensis, F. rubra and Poa pratensis.

L. pratensis in vegetation on sand in Western Europe

In the subocean heaths in the north-western parts of Europe L. pratensis was rare. At Voldum, Jylland, Denmark (PEB) diploid L. pratensis grew on the Calluna heath in a spot dominated by Deschampsia flexuosa and including Carex arenaria, Festuca pratensis, Holcus lanatus, Salix repens and Vicia cracca.

On a sand-field in Jylland, Denmark (PEJ), where Holcus lanatus was abundant, besides diploid L. pratensis the following species occured: Achillea millefolium, Artemisia vulgaris, Daucus carota, Equisetum arvense, Hieracium umbellatum, Rumex acetosella, Vicia angustifolia and V. cracca.

The most northern locality of tetraploid L. pratensis found in this investigation on the European continent is situated in Holland at Vogelsang (PHL) on the inner dunes, where otherwise only Agropyron junceum x pungens grew. However, in the same area tetraploid L. pratensis also grew at a canal-bank (PHK).

L. pratensis in vegetation on calcareous soils

In large parts of Europe L. pratensis was found in scattered localities in vegetation with species that prefer calcareous soils. Such plant communities were found e. g. in Sweden (PCQ, PCS) and Denmark (PFA) and more often in the southern parts of Europe (PUK, PVS, PXC, PXQ). Only two tetraploid samples of L. pratensis were found in Yugoslavia, both on calcareous ground. At Cricvenica (PXQ) Gladiolus sp, Lotus corniculatus, Salvia pratensis, Tragopogon pratensis, Bromus tectorum and Koeleria glauca were characteristic. In Yugoslavia, from that geographical zone, where localities of L. binatus and L. hallersteinii were found nearest each other (Pantocsek 1874) L. pratensis var. densifolius was described from meadows on serpentine at Čajetina, mountain Zlatibor, Yugoslavia (Novák 1923). The plant community was composed of many species (Table 13, PYO) and was probably

Table 13. Survey of the vegetation of some localities of *Lathyrus hallersteinii* (HAB, HAF, HAH, HBC), *L. binatus* (BAE, BAA) and *L. pratensis* (PYO, PUE) in Yugoslavia and Roumania. Cf. the text. Only species with the frequency ≥ 40 % in at least one of the localities are listed in the table.

Collection no.	HAB	HAF	HAH	HBC	BAE	BAA	PYO	PUE
Date 1965	05-11	05-13	05-17	05-21	05-24	05-26	05-23	05-19
Degree of cover of trees (%)	95	90	100	90	40	0	0	0
Naked ground area (%)	45	55	10	20	40	50	0	0
Inclination (o)	0	5	15	10	35	30	0	5
Corylus avellana	73^{3}	-	-	-	-	-	-	-
Anemone nemorosa	93^{1}	-	13^{x}	-	-	-	-	-
Agoseris foetida	80^{1}	13^{x}	7^{x}	-	-	-	-	-
Viola sylvestris	87^{x}	13^{x}	-	20^{x}	-	-	-	-
Melampyrum bihariense	47^{x}	47^{x}	27^{x}	-	-	-	-	-
Dactylis glomerata	40^{1}	53^{x}	-	13^{x}	-	-	-	-
Carpinus betulus	53^{4}	47^{2}	33^{3}	7^{x}	-	-	-	-
Stellaria holostea	53^{x}	87^{1}	47^{x}	-	-	-	-	-
Galium schultesii	33^{x}	47^{x}	33^{x}	-	-	-	-	-
Lathyrus vernus	7^{1}	33^{x}	13^{x}	40^{1}	-	-	-	-
Veronica chamaedrys	47^{x}	13^{x}	53^{x}	-	-	-	93^{1}	-
Luzula sylvatica	27^{x}	-	100^{1}	-	-	-	-	-
Galium cruciata	13^{x}	47^{x}	67^{x}	7^{x}	-	-	-	-
Poa nemoralis	47^{x}	67^{x}	47^{x}	33^{x}	-	-	-	-
Fagus sylvatica	13^{1}	-	27^{1}	-	-	-	-	-
Cytisus nigricans	13^{x}	13^{x}	93^{x}	7^{x}	-	-	-	-
Melica uniflora	20^{x}	87^{x}	67^{x}	53^{x}	-	-	-	-
Quercus petrea	93^{4}	75^{5}	93^{5}	93^{4}	7^{x}	-	-	-
Lathyrus hallersteinii	7^{x}	7^{x}	7^{x}	13^{x}	-	-	-	-
Fraxinus excelsior	-	7^{x}	-	53^{1}	-	-	-	-
Cytisus leucotrichus	-	40^{x}	27^{x}	7^{x}	87^{x}	-	-	-
Quercus cerris	-	33^{5}	47^{4}	53^{4}	40^{2}	-	-	-
Crataegus monogyna	13^{1}	13^{x}	-	73^{1}	67^{1}	-	-	-
Cotinus coggygria	-	-	-	-	80^{3}	-	-	-
Fraxinus ornus	-	-	-	-	73^{3}	-	-	-
Quercus pubescens	-	-	-	-	53^{2}	-	-	-

Carex pilulifera	-	-	-	-	87^{1}	27^{1}	-	-
Erica sp.	-	-	-	-	60^{x}	73^{1}	-	-
Bromus sp.	-	-	-	-	47^{x}	67^{2}	-	-
Lathyrus binatus	-	-	-	-	13^{x}	53^{1}	-	-
Sedum sp.	-	-	-	-	-	53^{1}	-	-
Festuca ovina	-	-	40^{x}	-	7^{x}	47^{x}	60^{2}	40^{x}
Thymus serpyllum	-	-	-	-	33^{1}	87^{1}	53^{1}	-
Salvia pratensis	-	-	-	-	27^{x}	7^{1}	53^{1}	-
Sanguisorba minor	-	-	-	-	27^{x}	60^{1}	93^{1}	-
Poa pratensis	-	-	-	33^{x}	-	40^{1}	33^{1}	53^{1}
Achillea millefolium	-	-	-	13^{x}	-	-	87^{1}	33^{x}
Carex caryophyllea	-	-	-	-	-	7^{x}	87^{1}	-
Prunella vulgaris	-	-	-	-	40^{x}	13^{x}	47^{x}	80^{1}
Trifolium campestre	-	-	-	-	-	-	100^{1}	-
Rhinanthus rumelicus	-	-	-	-	-	-	80^{2}	-
Poa annuua	-	-	-	-	-	-	60^{1}	-
Galium verum	-	-	-	-	-	13^{x}	60^{x}	27^{x}
Myosotis arvensis	-	-	-	-	-	-	60^{x}	33^{x}
Lotus corniculatus	-	-	-	-	-	7^{x}	100^{1}	47^{x}
Trifolium repens	-	-	-	-	-	-	67^{1}	53^{x}
Cerastium semidecandrum	-	-	-	-	-	-	67^{x}	53^{x}
Plantago lanceolata	-	-	-	-	-	-	67^{1}	67^{x}
Anthoxanthum odoratum	-	-	-	-	-	-	73^{1}	100^{1}
Lathyrus pratensis	-	-	-	-	-	-	60^{x}	87^{1}
Ranunculus acris	-	-	-	7^{x}	-	-	60^{1}	100^{1}
Chrysanthemum leucanthemum	-	-	-	-	-	-	40^{x}	67^{x}
Rumex acetosa	-	-	-	-	-	-	20^{x}	67^{x}
Lythrum salicaria	-	-	-	-	-	-	-	53^{1}
Carex hirta	-	-	-	-	-	-	-	53^{x}
Lysimachia vulgaris	-	-	-	-	-	-	-	47^{1}

favoured by a suitable nutrient supply with, according to soil analyses, relatively high contents of, e.g., magnesium, potassium and phosphate.

PLANT COMMUNITIES WITH LATHYRUS BINATUS

L. binatus is recorded from scree slopes on serpentine in Bosna, Hercegovina and Serbia in Yugoslavia. The localities of L. binatus studied in this investigation were usually exposed and characterised by no close vegetation and relatively few herbs and usually few (e.g. BAA) shrubs and trees. Sometimes the plants were covered by fallen stones on the relatively steep slopes. Often L. binatus grew in the protection of tussocks of Bromus (Table 13, Fig. 24) on levels up to 1800 m (cf. Ritter v. Beck 1874).

At Sarajevo L. pratensis was found in meadow vegetation only 60 m. away from a locality of L. binatus (BAA). No hybrids were found anywhere between these two taxa.

PLANT COMMUNITIES WITH LATHYRUS HALLERSTEINII

L. hallersteinii is distributed in Roumania and Yugoslavia, commonly within woods of dominating Quercus (seldom Fagus, Carpinus). The plant communities were relatively uniform, usually with a sparse vegetation in the field layer but often with a well-developed bush layer e.g. Acer campestre, Carpinus betulus, Cornus sanguinea, Corylus avellana, Crataegus monogyna, Cytisus leucotrichus, C. nigricans, Euonymus europaeus, Fagus silvatica, Ligustrum vulgare, Lonicera xylosteum, Malus sylvestris, Prunus avium, P. padus, Rhamnus cathartica, Syringa vulgaris (Table 13, Fig. 23). Thus, L. hallersteinii grew mainly in the shadow in forests composed largely of Quercus, while L. pratensis in the same areas was found exposed in forest margins in close vegetation. No crosses between L. pratensis and L. hallersteinii were found.

SOIL ANALYSES

The results of some chemical analyses of soil samples of localities of tetraploid and diploid L. pratensis, L. binatus and L. hallersteinii show in general a more wide variation in L. pratensis thanin the two other taxa (Fig. 25). The few samples analysed of L. binatus were more similar, with e.g. relatively high pH-values as well as calcium content, while the magnesium content was low. Evidently, L. binatus prefers calcareous soil but hardly serpentine, as earlier has been reported. One sample with a relatively high magnesium content was from the locus classicus of L. pratensis var. densifolius Nowák (PYO), on serpentine (p. 62). The two high values of sodium were from two extreme localities, viz. tetraploid L. pratensis (PHM) on the inner dunes on original marine land in the Netherlands and L. hallersteinii (HAC) on saline soil in Roumania. The soils analysed of L. hallersteinii had higher manganese content than the soils of the other taxa and had often a higher loss on ignition.

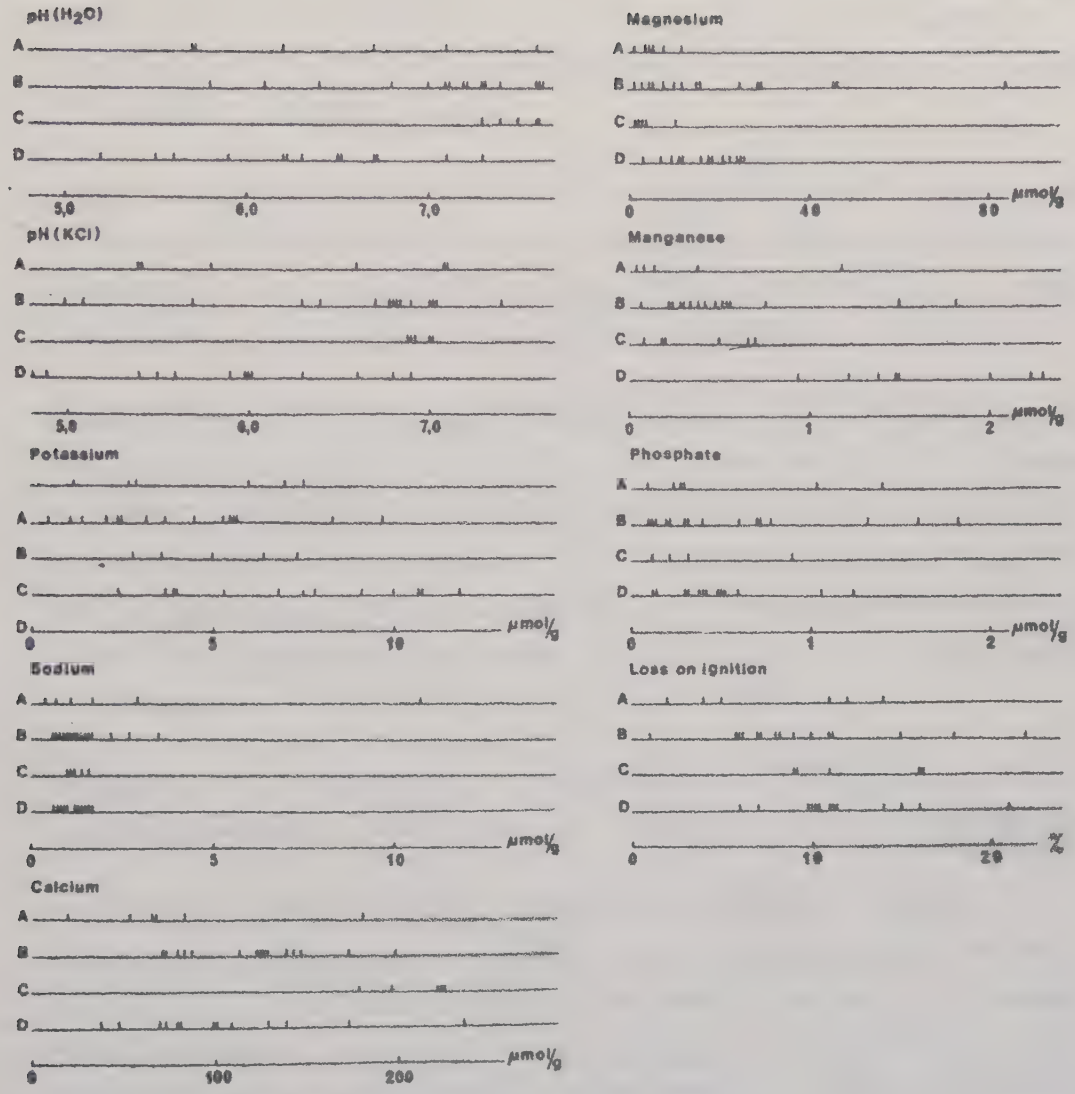


Fig. 25. Variation in dried soil samples from different localities. -- A: Lathyrus pratensis 2n=28 (PHK, PHL, PHM, PJG, PSH, PXQ). -- B: L. pratensis 2n=14 (PEY, PHE, PLM, PND, PNF, PPM, PTB, PUA, PUK, PVN, PVS, PXC, PYK, PYN, PYO). -- C: L. binatus (BAA, BAB, BAD, BAE, BAF). -- D: L. hallersteinii (HAA, HAB, HAC, HAD, HAE, HAF, HAG, HAH, HAJ, HAK, HBB, HBC, HBD).

X. MORPHOLOGIC VARIATION

The aim of the morphological investigation of the L. pratensis complex was to elucidate by biometric studies the degree of genetical and modificative variation, in morphological characters of supposed taxonomic value.

A previous taxonomic division of L. pratensis was based on degree of hairiness etc. Comparative cultivations showed that in some populations hairiness was genetically determined and in others modificative, and thus of no taxonomic value.

The habitat of L. pratensis varies greatly in different parts of the European area of distribution (cf. chapter IX). Differences various morphological characters may occur between populations situated very close to each other. Interpopulational variation in the L. pratensis complex in Europe is difficult to elucidate in a simple but comprehensive manner in a survey of the whole complex in Europe.

Morphological characters in populations of L. pratensis L. did not show variation which permits a subdivision into subspecies.

Variation in morphological characters between tetraploid and diploid L. pratensis, L. binatus and L. hallersteinii before and after cultivation under uniform conditions will be compared organ by organ. L. sepium and L. lusseri are included in L. pratensis as no morphological, cytological or other differences were found.

MATERIAL

The biometric studies were based on dried material collected in the field as well as shoots of the same plants cultivated under uniform conditions for (2--) 3--4 (--5) years. Material from about 45 tetraploid and 70 diploid populations of L. pratensis from representative parts of the European distribution area were used (Fig. 26). Available, well-developed herbarium material of L. binatus and L. hallersteinii (Appendix II) was included in the comparative study as the authors samples of these taxa were relatively small.

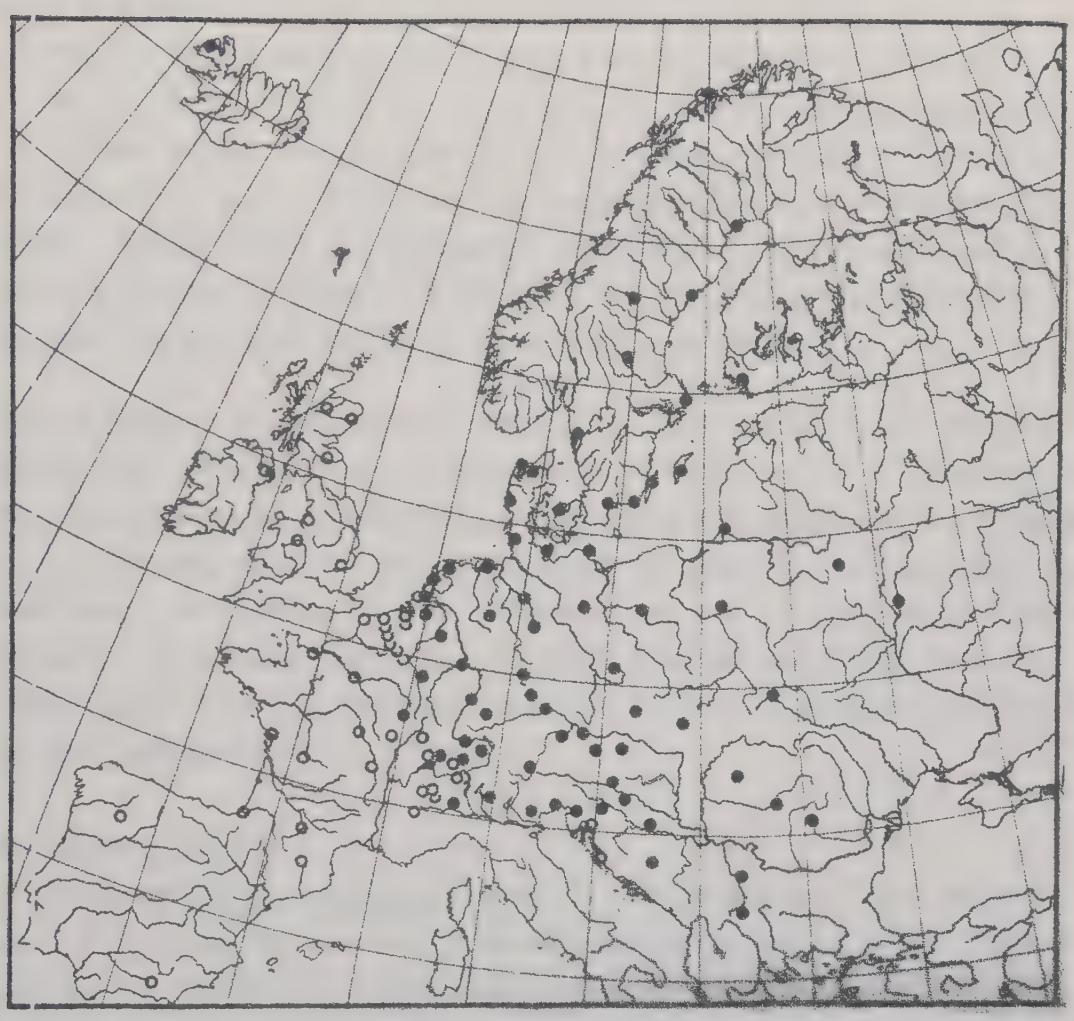


Fig. 26. Lathyrus pratensis. Localities of morphologically investigated samples. Circles represent tetraploids, dots diploids.

METHODS

Figure 27 serves to show essentially how the size of various parts has been calculated. The leaflets and the stipules were measured macroscopically while the other parts were measured under a binocular preparation microscope with scale units of 1/6 mm. Plastids were stained in 1 % $AgNO_3$ solution. Control of the greatest lengths of the guard cells and the pollen grains (in cotton blue) was carried out in a Leitz microscope with a precisions of 2.5×10^{-3} mm. The largest diameter of the pollen grains (polar view) was measured. Floral parts were measured on flowers boiled in water for a short while. They were dissected out and placed on a slide on a drop of glycerine.

The results of the biometric studies of the morphologic variation within and between ploidy levels and taxa are shown in diagrams and histograms. No statistical treatments are given as the diagrams and histograms as such are considered to show the modificative and genetical variation. In the diagrams the per cent distribution is indicated by graded hatching. In each diagram and histogram the number of plants (n) examined and the number of samples (N) included are mentioned.

RHIZOMS AND SHOOTS

All taxa in the L. pratensis complex are perennial. The aerial parts wither in the autumn. Renewal of growth takes place from buds on the subterranean rhizomes. Flowering shoots are not usually produced until the second vegetation period. The vegetative development from seed to young plant in Lathyrus varies greatly (cf. Gluch 1971).

The length of the rhizomes was very variable depending on age and vitality of the plant. Rhizome length varied greatly from year to year within a plant and among plants in the same population. In cultivation, rhizomes up to 7 m were found. One spontaneous triploid population (coll. PCG), which probably consisted of clone individuals, covered an area of 25 x 10 metres. However, no significant difference between populations or taxa was found.

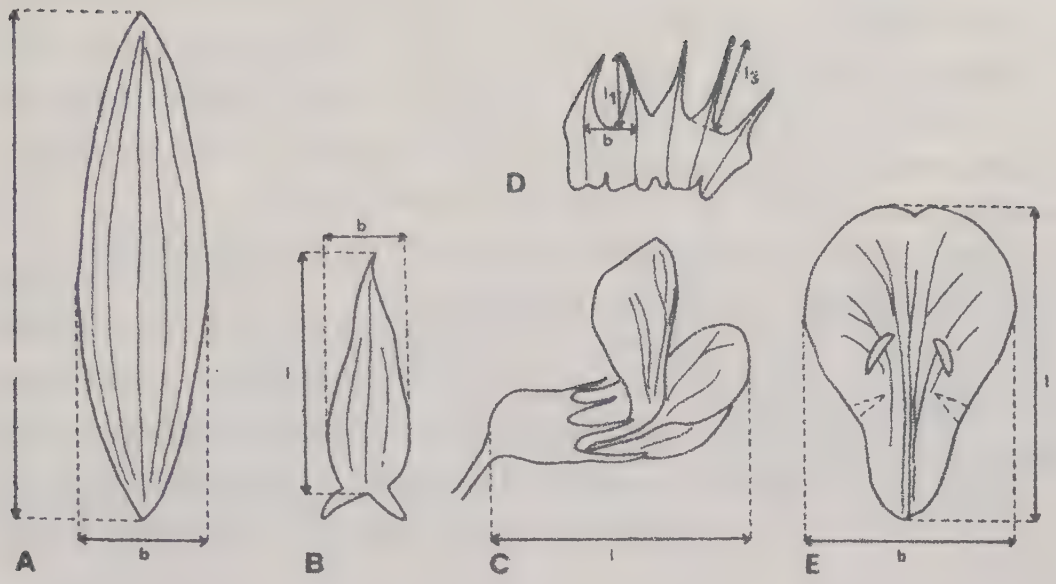


Fig. 27. Measurements of length (l) and breadth (b). -- A: Leaflet. -- B: Stipule. -- C: Flower. -- D: Calyx. -- E: Standard.

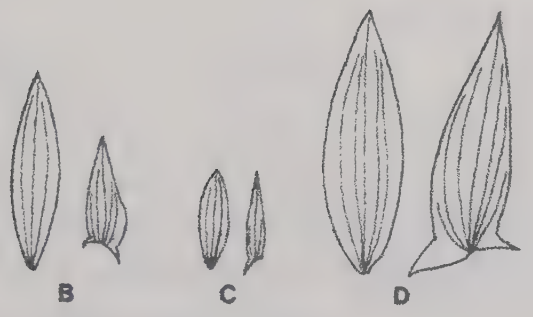


Fig. 28. Leaflets and stipules. -- B: Lathyrus pratensis. -- C: L. binatus. -- D: L. hallersteinii.

Shoots of diploid as well as of tetraploid L. pratensis are (30--) 50--90 cm. and often erect but climbing. No differences were found between the two ploidy levels. Stems of L. binatus are normally not more than 10--25 cm tall and more or less decumbent, while the shoots of L. hallersteinii are more erect with a length of about 20--40 (--50) cm. The shoots are glabrous in L. hallersteinii, glabrous to almost glabrous in L. binatus but usually ± pubescent in L. pratensis. Often the shoots are fewer in number in L. hallersteinii than in the other taxa. However, the modificative variation in this character is wide. In experiments with repeated cutting of originally erect plants of L. pratensis, the plants acquired a decumbent habit and developed a larger number of shoots than the original plants.

LEAVES

All taxa in the L. pratensis complex have leaves with one pair of leaflets and a rachis ending in a single or ramified tendril as in L. pratensis and in L. hallersteinii or a tip only as in L. binatus. The leaflets of all taxa in the L. pratensis group are elliptic to lanceolate and parallelly veined. The greatest length and width were measured (Fig. 27) of the leaflets in the axil of which the lowest raceme is situated. Usually 5--10 plants of each population were measured.

The intraindividual and intrapopulational variation was wide in the spontaneous material but less in the cultivated material. Differences in average size between different samples were often distinct, even in cultivation. No differences between material from different areas were found.

L. binatus on the average had considerably smaller leaflets than the others, while L. hallersteinii had larger leaflets and the spontaneous material in particular showed more variation (Fig. 29). However, there was considerable overlapping between taxa. Diploid and tetraploid L. pratensis showed small differences.

STIPULES

Stipule length was measured from the stem to the stipule apex (Fig. 27). Thus, the basal lobes were not included. The stipules were taken in the axil of the lowest raceme.

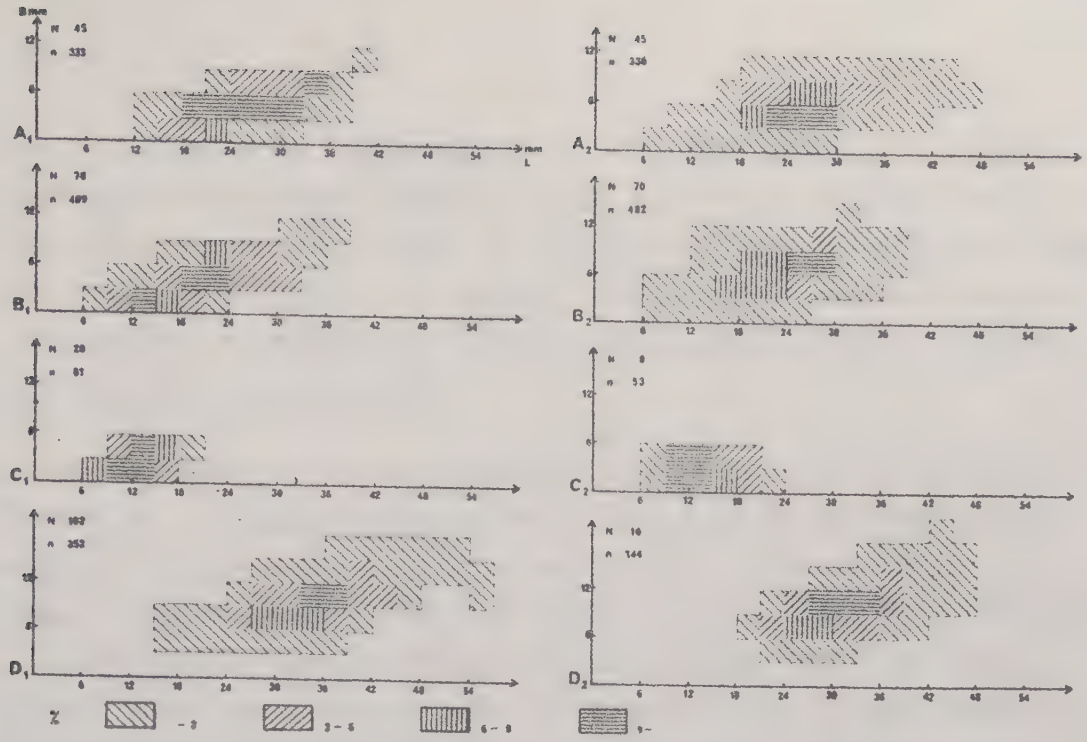


Fig. 29. Length (horizontal axis) and breadth (vertical axis) of leaflets of herbarium material (left) and cultivated material (right). Means of 2—4 measurements per plant. — A: Lathyrus pratensis 2n=28. — B: L. pratensis 2n=14. — C: L. binatus. — D: L. hallersteinii.

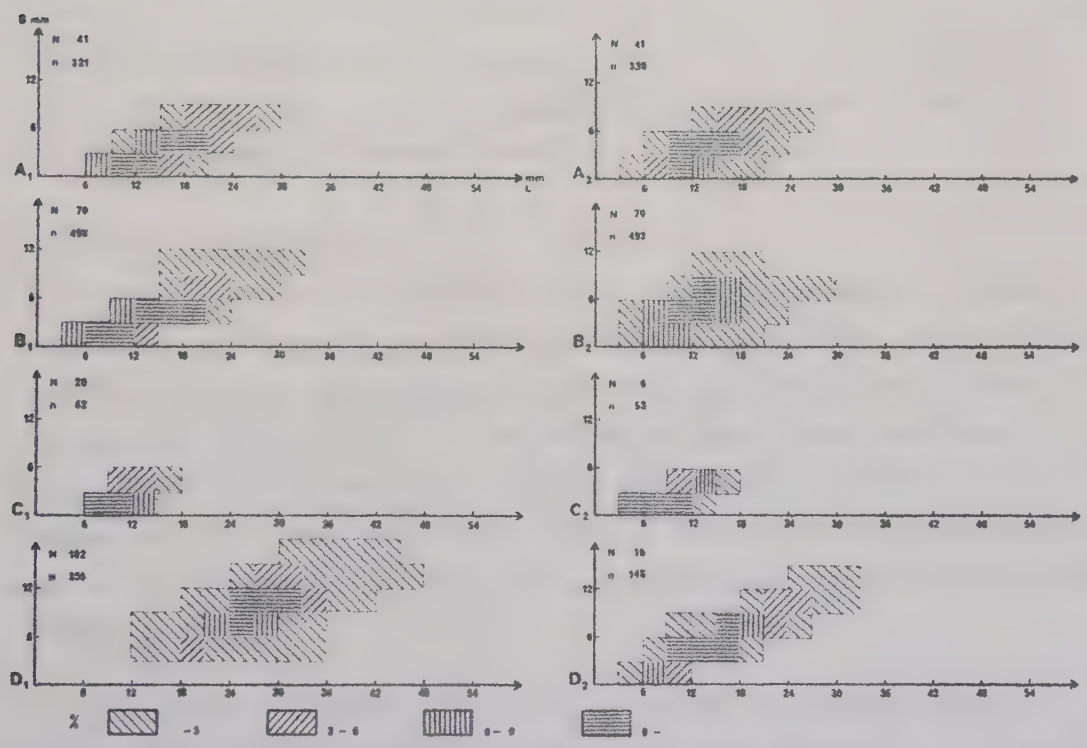


Fig. 30. Length (horizontal axis) and width (vertical axis) of stipules of herbarium material (left) and cultivated material (right). Means of 2—4 measurements per plant. — A: Lathyrus pratensis 2n=28. — B: L. pratensis 2n=14. — C: L. binatus. — D: L. hallersteinii.

The stipules of L. hallersteinii in the spontaneous material in particular were larger and above all as a rule broader than in the other comparative taxa. L. binatus had smaller stipules than the other taxa. They were usually both shorter and more narrow. There were no significant differences in size between tetraploid and diploid L. pratensis.

After cultivation the differences between taxa were less marked. Plants of L. hallersteinii after 2--3 years of cultivation had smaller stipules and leaflets than on the original shoots. The reason for this may be the environment that may be less favourable in cultivation than in nature for this taxon, which naturally grows in the south-eastern parts of Europe and in more shady habitats with a higher humidity. The diagrams indicate that the vegetative development of stipules and leaflets on the whole is relatively modificative. However, the stipules differ in shape in the studied taxa (Fig. 28). They are almost symmestrical at the base and always have two basal lobes in L. pratensis and L. hallersteinii, while in L. binatus they often have one basal lobe only, which makes the base asymmetrical (Fig. 30). The basal lobes of each of the stipules are placed at a acute angle and are directed downwards in L. pratensis as well as in L. binatus if there are two lobes. In L. hallersteinii the basal lobes are directed outwards ± rectilinearly.

EPIDERMIS AND STOMATA

The structure of the epidermis is of certain taxonomic value in some species in Lathyrus (Senn 1938a, Bässler 1966, 1973, Simola 1968). In the L. pratensis complex the epidemical cells have undulating walls (Fig. 37) and stomata were found scattered on both sides of the leaflets, though more sparsely above. The number of epidermal cells and stomata was found to be very variable and of no taxonomic value in the L. pratensis complex as in Orobus (Bässler 1973).

No particular difference in size or shape of stomata between abaxial and adaxial sides of the leaves was noticed in the material of the L. pratensis complex. The greatest stomata length, defined

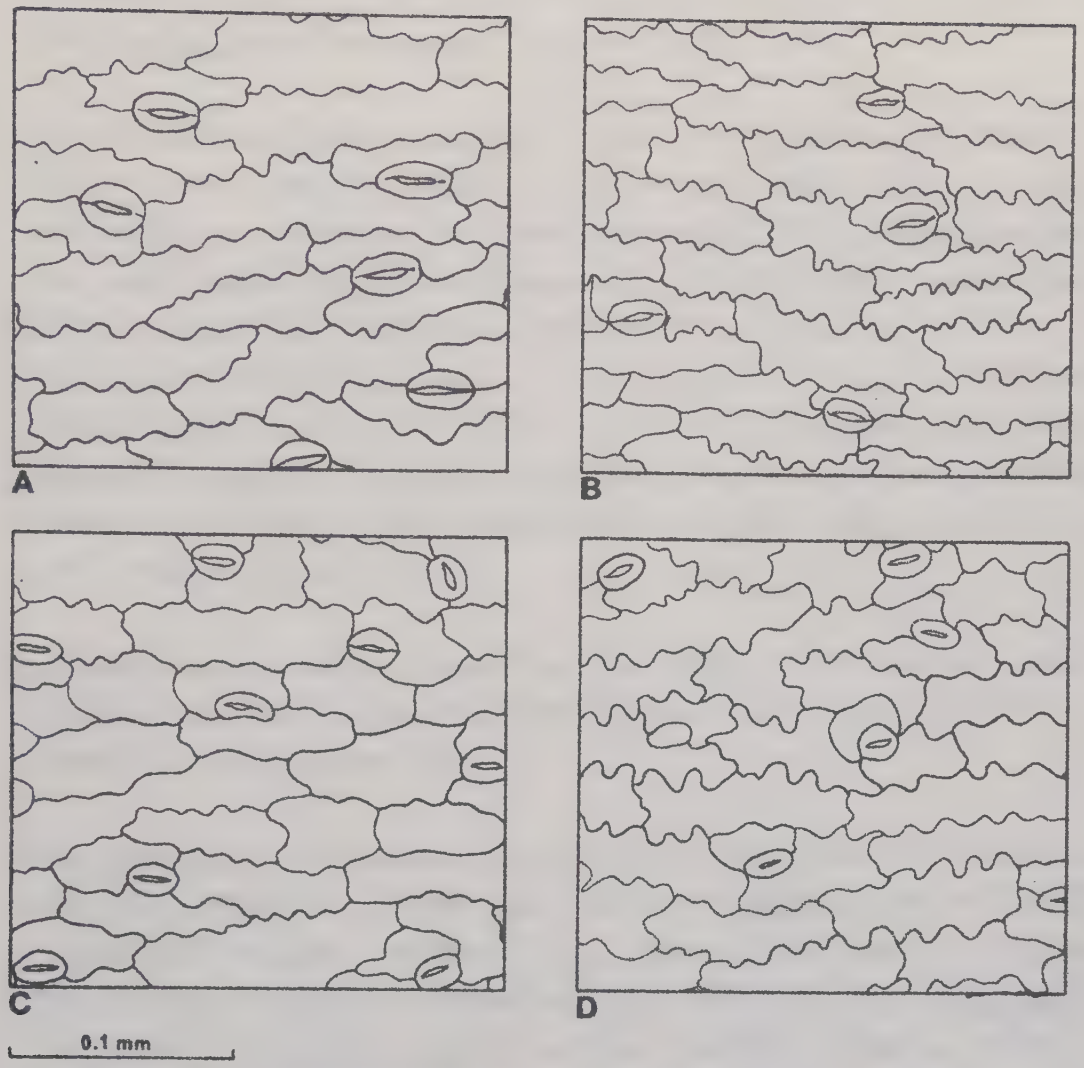


Fig. 31. Epidermis cells from the abaxial side of a leaflet. -- A: Lathyrus pratensis 2n=28 (PSH:13). -- B: L. pratensis 2n=14 (PBB:2). -- C: L. binatus (BAB:3). -- D: L. hallersteinii (HBE:13).

as the length of the guards cells, was measured on epidermis taken from the abaxial side of the leaflets. Leaves supporting the lowermost raceme were used. The plants were grown open in the gardens under as uniform conditions as possible to eliminate modificative variation depending on exposure or shade as occurs e.g. in L. palustris (Brunsberg, unpublished).

The intraindividual variation in the group was small. Thus, a test of the stomatal length from the under side of the leaves on different shoots of the same specimen (PTN:1) expressed as the mean value of ten measurements (in μ) on every second leaflet from the base and upwards showed shoot 1: 12.5, 11.9, 12.0, 11.2, 10.7, 9.2; shoot 2: 11.7, 11.5, 11.3, 11.1, 10.6, 9.7 and shoot 3: 12.0, 12.1, 12.2, 11.7, 11.7, 11.2, 10.9, 11.1 and 10.1. The stomatal length of the upper and undeveloped leaflets is smaller than on the others. No correlation was found between leaflet size and stomatal length.

A comparison between stomata on the adaxial and abaxial sides of the leaflets showed that the length was usually 1--3 μ shorter on the upper side.

A comparison of stomatal length in the same material after one and five years of cultivation, respectively, showed small differences of the mean values (0,5 μ). The mean values of the stomatal length were larger in tetraploid than in diploid L. pratensis (Fig. 32). L. hallersteinii had the smallest stomata, while L. binatus was intermediate in this character. No tendency to cline variation in Europe was found in L. pratensis but the material at respective ploidy level showed similar variation and had about the same differences in mean values in different parts of Europe.

PLASTIDS

In daylight the plastids in the guard cells were diffuse and impossible to observe. If the plants were placed in a dark room for some hours the plastids acquired a distinct form and were easily seen by staining. The number of plastids were often but not always the same in the two guard cells. They were 10--15

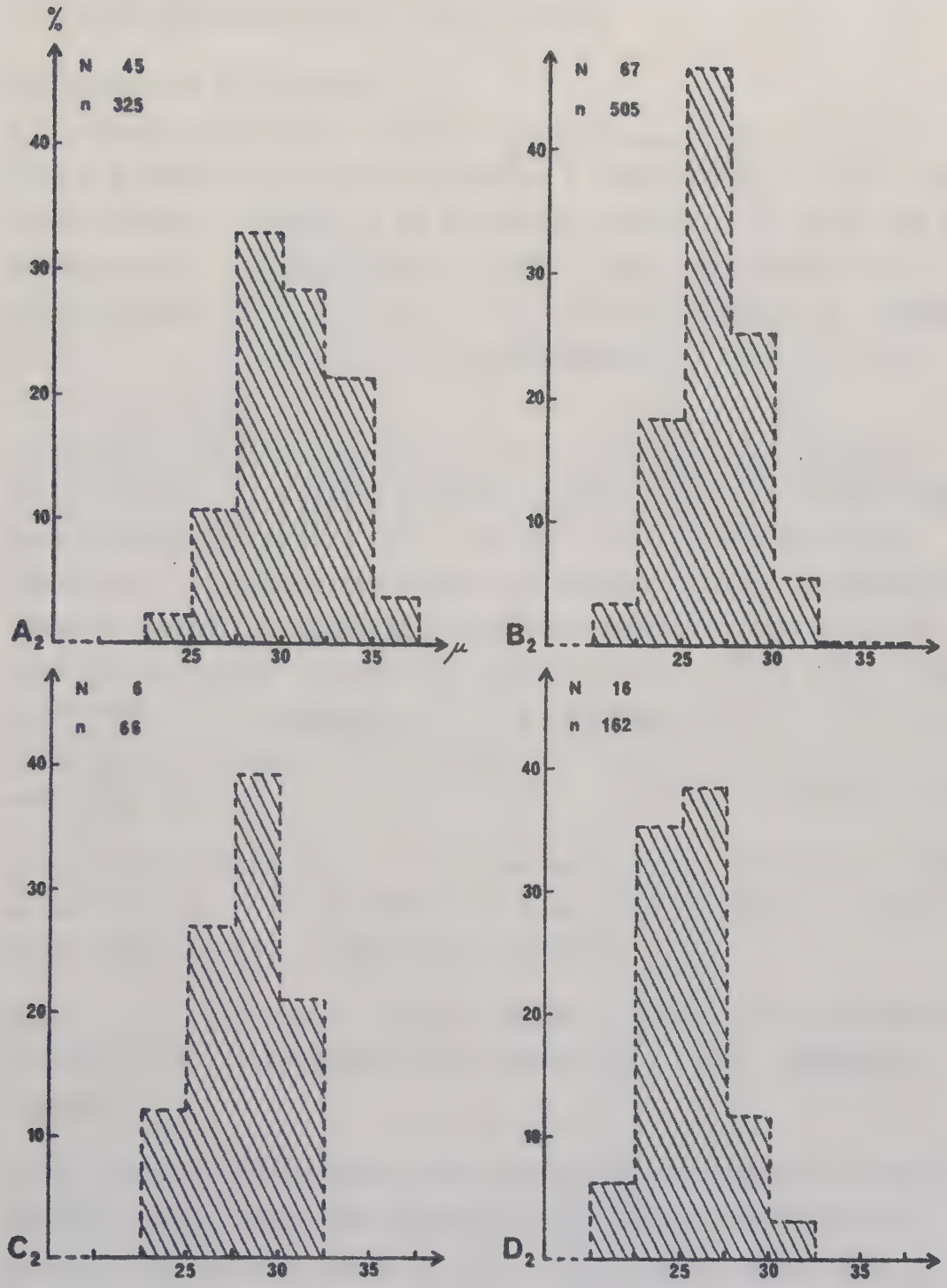
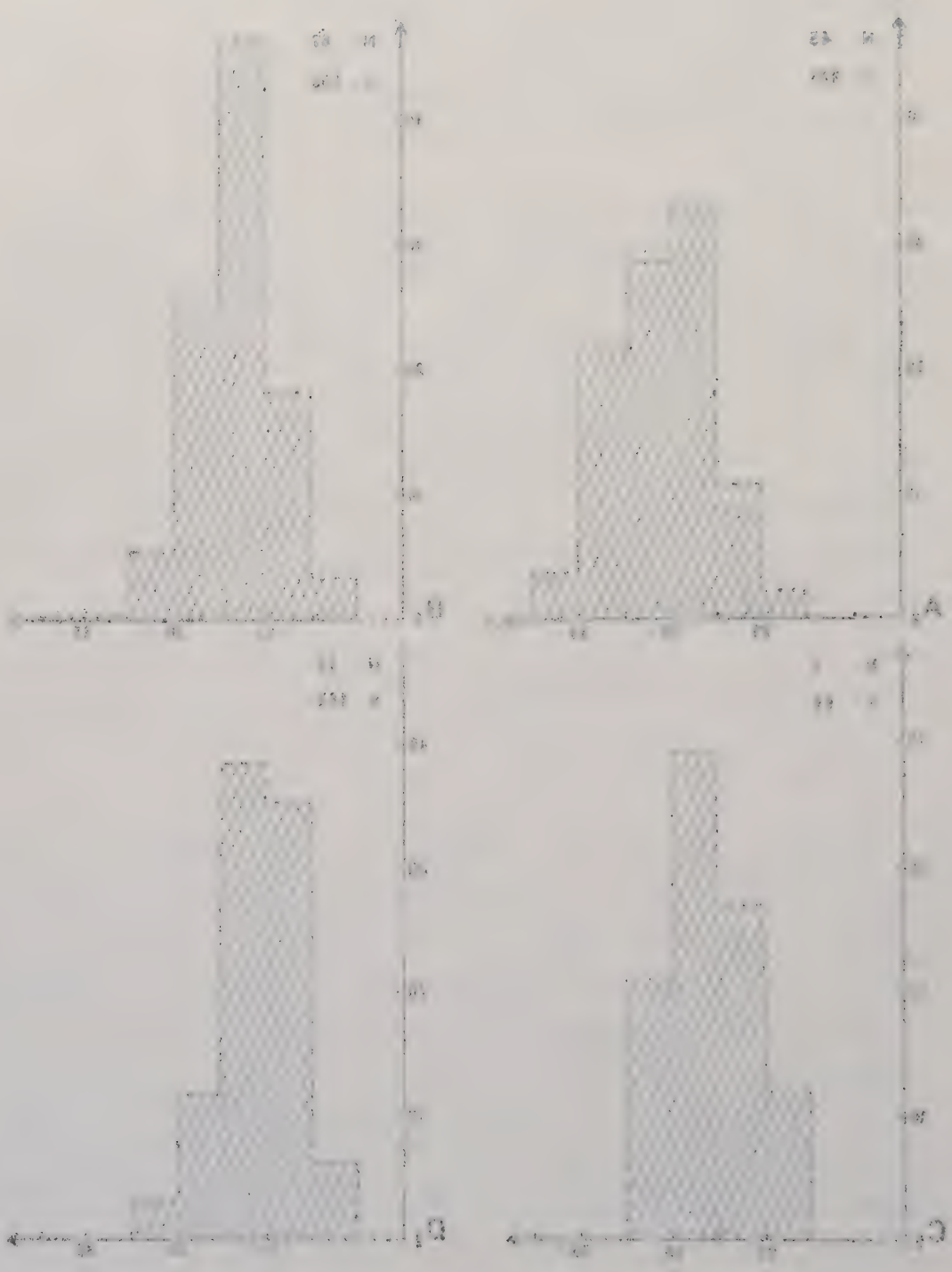


Fig. 32. Stomata length. Means of at least ten measurements per plant. Cultivated material. -- A: Lathyrus pratensis 2n=28. -- B: L. pratensis 2n=14. -- C: L. binatus. -- D: L. hallersteinii.



(--25) in number. No differences between ploidy levels and taxa in the L. pratensis complex were found.

INFLORESCENCE AND FLOWERS

The inflorescences are placed in multiflorous lateral racemes that are going out in the leaf-axis. A low number of flowers per inflorescense is regarded as a derived character in Vicia and in Lathyrus sect. Orobus (Bässler 1973). Within the complex, L. hallersteinii is characterised by unilateral racemes, L. binatus by pauciflorus racemes, while L. pratensis has many-flowered not unilateral racemes.

Diploids as well as tetraploids of L. pratensis commonly had 5--10 flowers, L. binatus 2--4 and L. hallersteinii usually had 3--6 flowers per raceme (Fig. 33). The overlapping was large. The number of flowers per raceme is somewhat larger in tetraploid than in diploid L. pratensis. After comparative cultivation in Lund the number of flowers per raceme was reduced to some extent in tetraploid L. pratensis and in L. binatus and more evidently in L. hallersteinii. Probably this is connected with the more deviating climate in relation to their natural distribution area.

The bracts and bracteoles 1 x 1--4 mm, that are sometimes lacking as well as the pedicels, about 2--5 mm. long or shorter, showed no differences in the L. pratensis complex.

The size of the flower (Fig. 27) usually showed little intraindividual and intrapopulational variation in the L. pratensis complex.

In L. pratensis some cases with noticeable differences in size between populations were registered. Generally, populations growing at high altitudes (> 1000 m) in the Alps often had proportionally larger flowers than populations growing in the valleys at lower altitudes in the neighbourhood. For the remainder, no definite trend in any direction was found. The flowers were of about equal size in diploid and tetraploid L. pratensis (Fig. 34). However, in the cultivation slightly larger flowers was found in diploid L. pratensis.

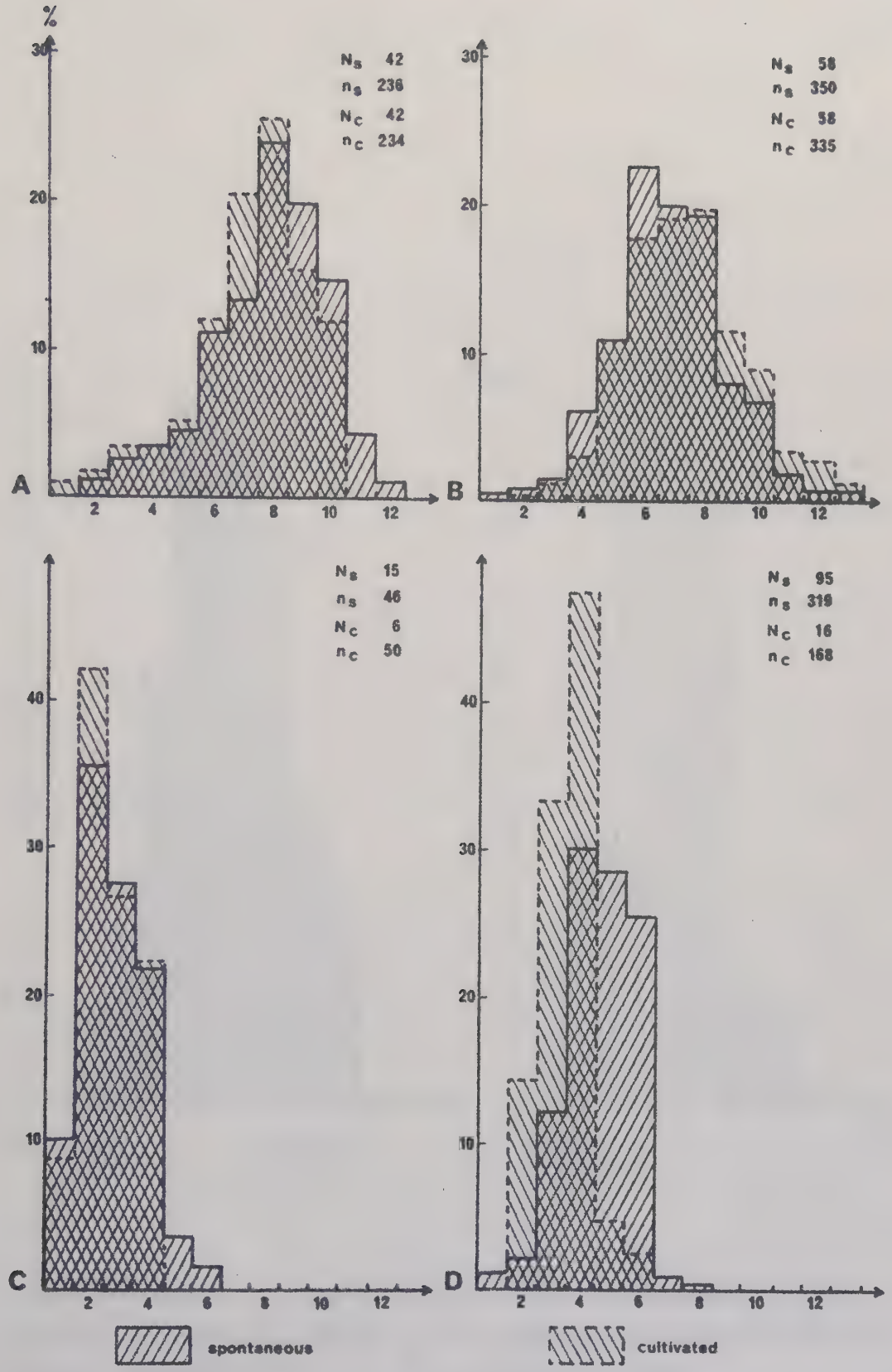
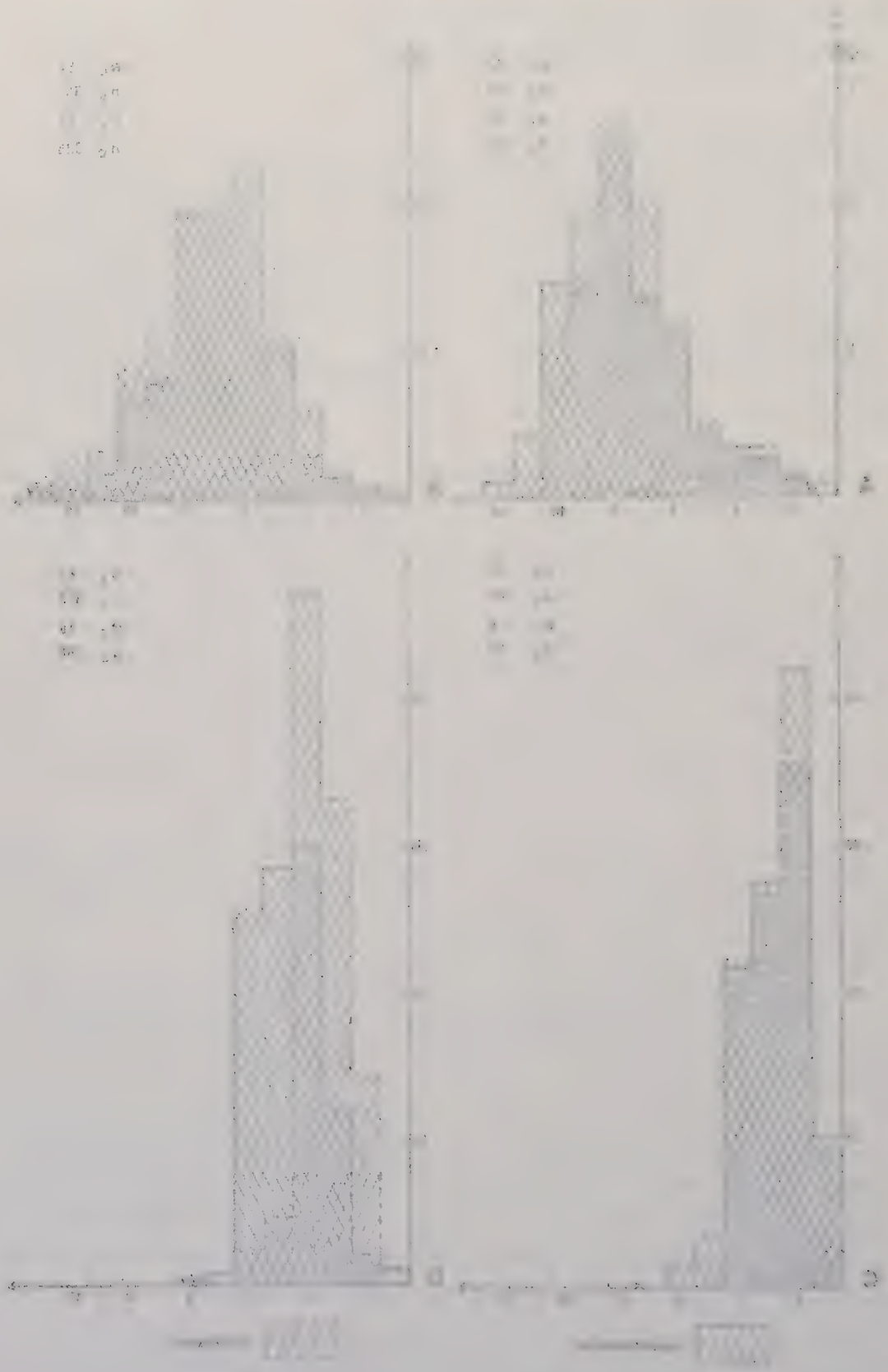


Fig. 33. Variation in the number of flowers per receme. Means of ast least 3 racemes per plant. -- A: Lathyrus pratensis 2n=28. B: L. pratensis 2n=14. -- C: L. binatus. -- D: L. hallersteinii.



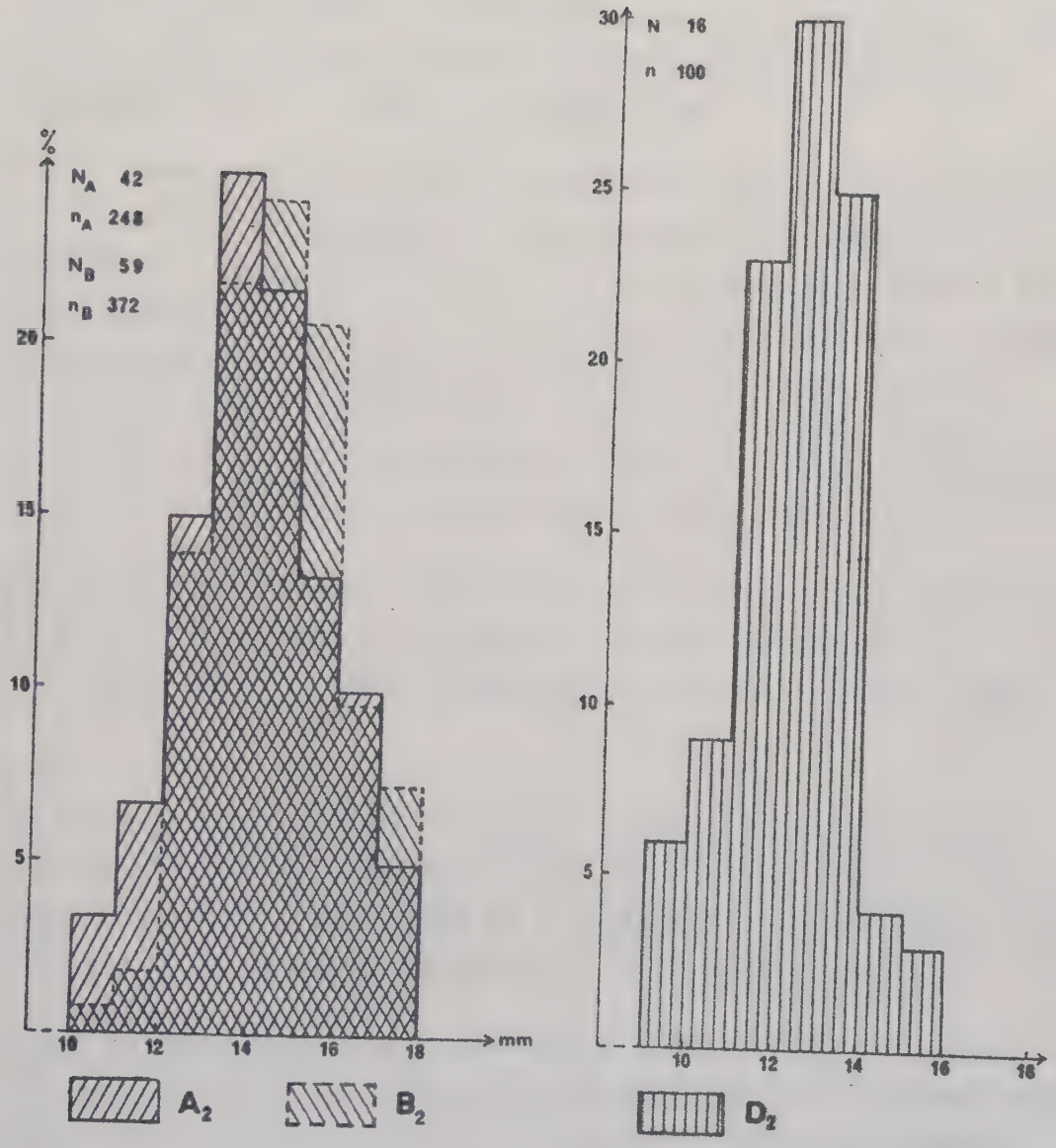


Fig. 34. Length of flower. Cultivated material. Means of at least 5 flowers per plant. -- A_2: Lathyrus pratensis 2n=28. -- B_2: L. pratensis 2n=14. -- D_2: L. hallersteinii.

L. hallersteinii had considerably smaller flowers than L. pratensis (Fig. 34), while the largest flowers in the complex were found in L. binatus, viz. 13--22 mm. long.

The size of the flowers has been used previously in the taxonomic division of the L. pratensis complex. Thus, L. lusseri Heer was characterised by large flowers and ± glabrous appearance. Löve & Löve (1956) on loose grounds suggested that tetraploid L. pratensis should be named L. lusseri Heer.

In the present investigation the author collected plants from the type locality of L. lusseri, viz. Hospenthal altitude 1550 m in Switzerland. The population at this place had large flowers and all the plants turned out to be tetraploid. Similarily, L. pratensis var. grandiflorus Bogenhard, sometimes regarded as a synonym of L. lusseri Heer, was studied on its type locality, Hausberg in Germany. The plants of that population, however, as well as all the studied samples from Germany, were diploid.

Populations with large flowers growing at high levels were found to be either diploid or tetraploid. It was impossible to distinguish diploids and tetraploids according to floral size.

CALYX

In the L. pratensis complex the two uppermost calyx lobes are shorter and the lower median one longer than the others. The calyx is usually ± pubescent in L. pratensis, glabrous to almost glabrous in L. binatus and glabrous in L. hallersteinii.

In the L. pratensis complex the ratio between the long lowest lobe and one of the short upper lobes has been used taxonomically (Fig. 27). A biometric study of this ratio showed the highest values in L. pratensis. L. hallersteinii had lobes of more equal length and L. binatus was intermediate (Fig. 35). As there was much overlapping between the taxa in this character, it has a restricted diagnostic value.

The relation between the length of each of the uppermost lobes and the distance between their midribs at the base of the lobes

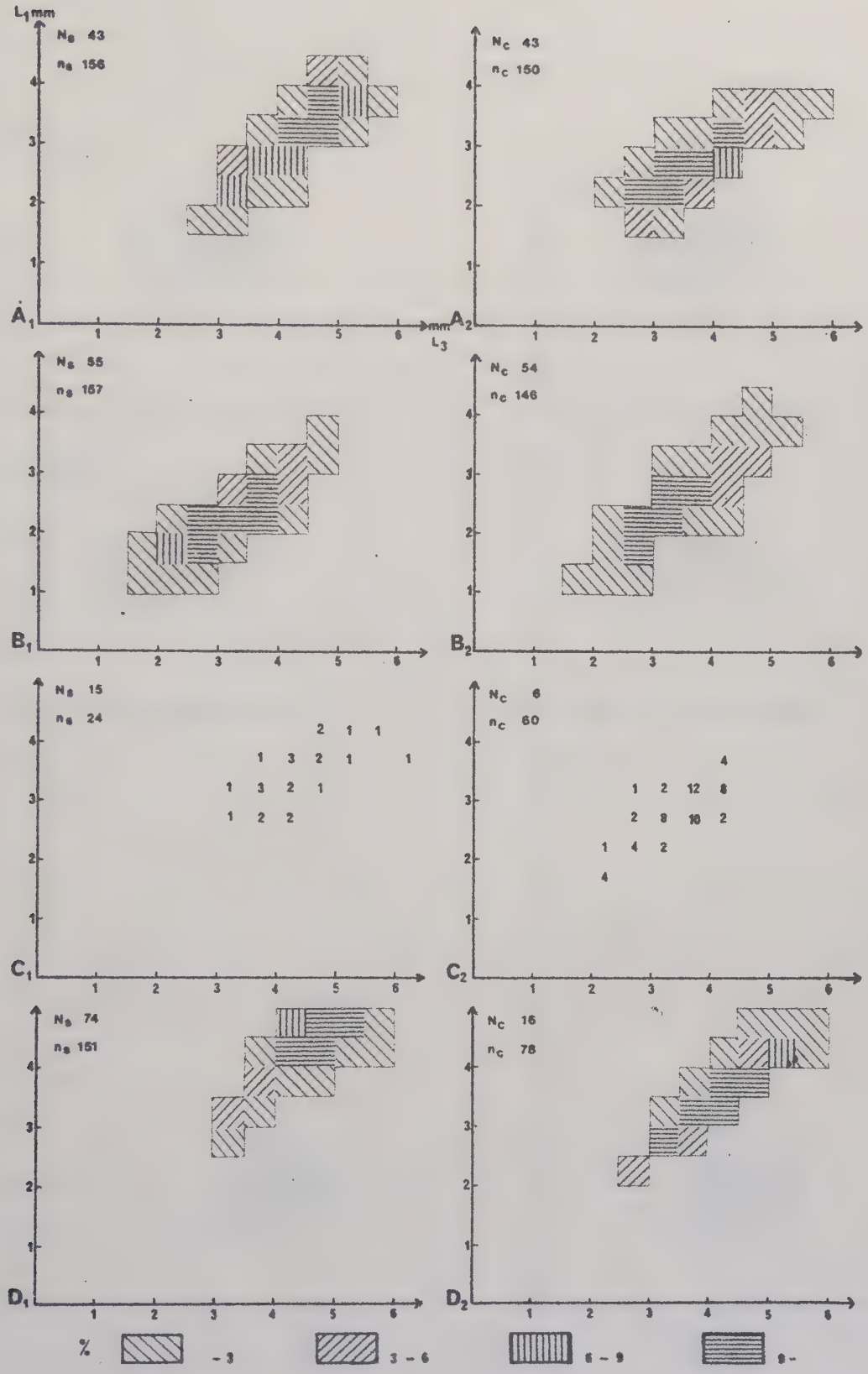


Fig. 35. Length of longest calyx lobe (horizontal axis) and one of the shortest lobes (vertical axis) of herbarium material (left) and cultivated material (right). Means of 5 measurements per plant. -- A: Lathyrus pratensis 2n=28. -- B: L. pratensis 2n=14. -- C: L. binatus. -- D: L. hallersteinii.

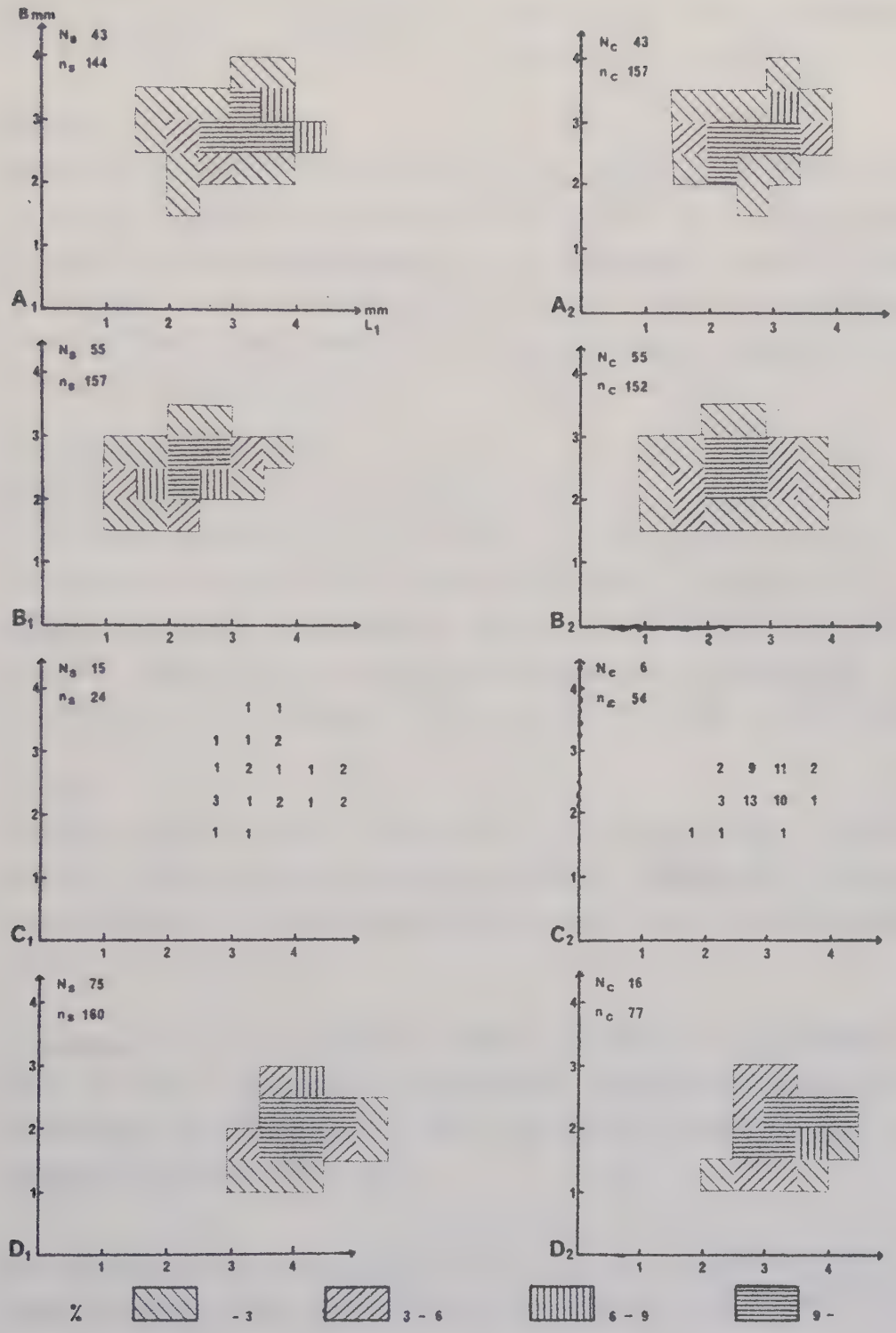


Fig. 36. Distance between the upper calyx lobes (vertical axis) and length of one of them (horizontal axis). Herbarium material (left) and cultivated material (right). Means of usually 5 measurements per plant. -- A: Lathyrus pratensis 2n=28. -- B: L. pratensis 2n=14. -- C: L. binatus. -- D: L. hallersteinii.

showed clear differences between the taxa (Fig. 36). L. hallersteinii had proportionally long upper lobes. Diploids and tetraploids of L. pratensis had proportionally shorter upper lobes and did not differ between each other. L. binatus was intermediate between the two species mentioned.

COROLLA

The petal colour is light yellow in L. binatus, which also lacks the violet veins often present of the petals of L. pratensis and rarely in L. hallersteinii. In L. pratensis several individuals in the same population were often found to have similar violet lines. On the other hand, the interpopulational variation in this character was wide and showed no obvious trend.

The standard was usually larger and particularly wider in L. pratensis than in L. hallersteinii while L. binatus had a somewhat larger vexillum than the two other taxa (Figs. 37, 38). The difference in size of the standard between L. binatus and L. hallersteinii was considerable. There was no significant difference in petal size between diploid and tetraploid L. pratensis. It was not possible to distinguish any taxa by the shape of the petals.

POLLEN

Detailed palynological studies of a few slides of the included taxa and ploidy levels did not reveal any substantial differences. The tricolporate pollen grains are indeed fairly smooth without special wall structure.

Measurements of the largest diameter as well as the shortest diameter of the ± ellipsoid pollen grains showed only small or no differences in form between taxa and ploidy levels in the L. pratensis complex (Fig. 39).

The length of the pollen grains did not vary notably within and between plants while the differences between samples were larger (cf. Fig. 40).

A noteworthy variation in pollen size was found in the same cultivated material of L. pratensis that was studied different years (Fig. 41). As a rule the average size of the pollen grains was 1--4 μ larger in material cultivated 5 years in the Botanical Gardens in Lund.

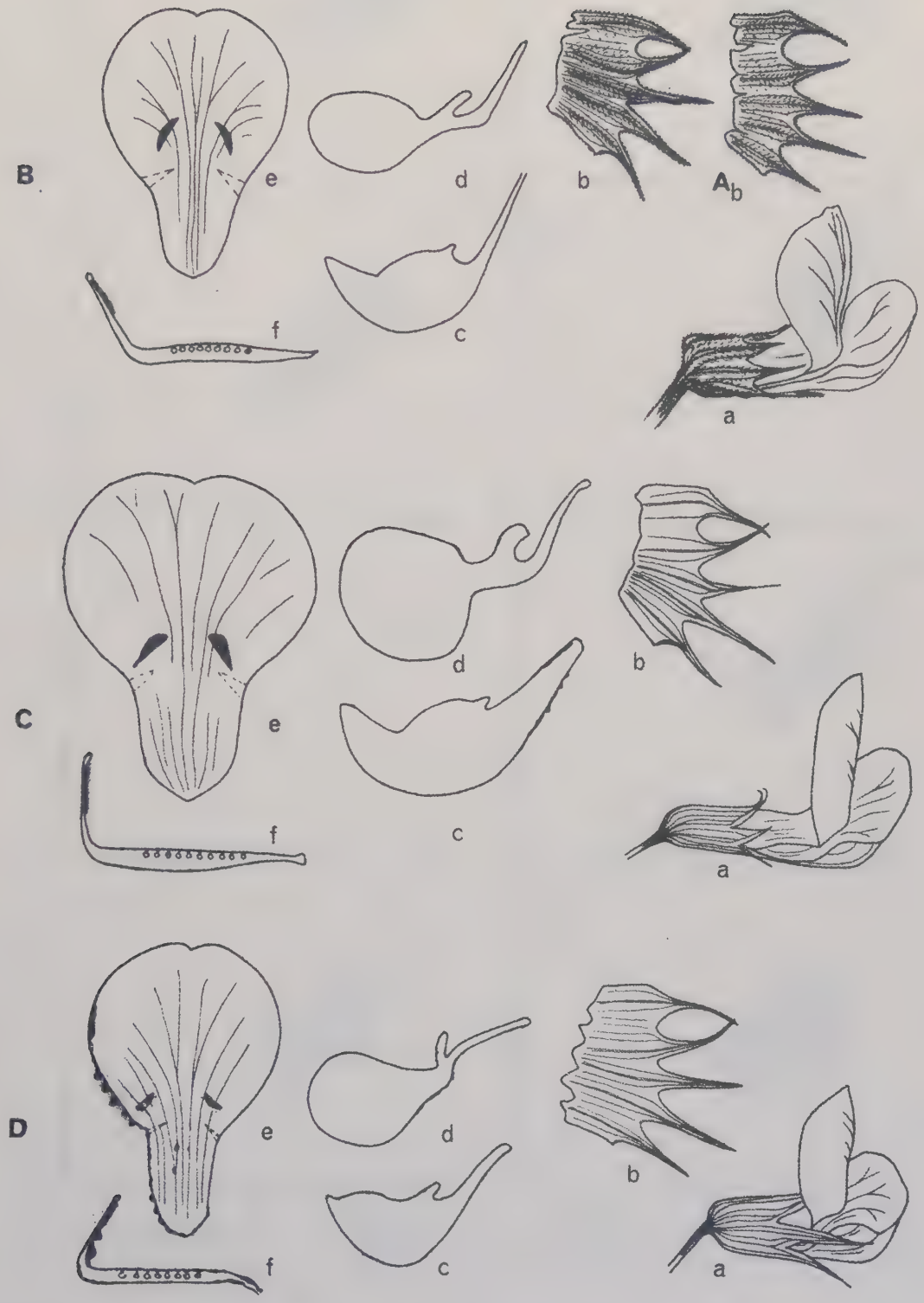


Fig. 37. Flower (a), calyx (b), carina (c), ala (d), vexillum (e) and gynoecium (f). -- A: Lathyrus pratensis 2n=28 (only calyx). -- B: L. pratensis 2n=14. -- C: L. binatus. -- D: L. hallersteinii.

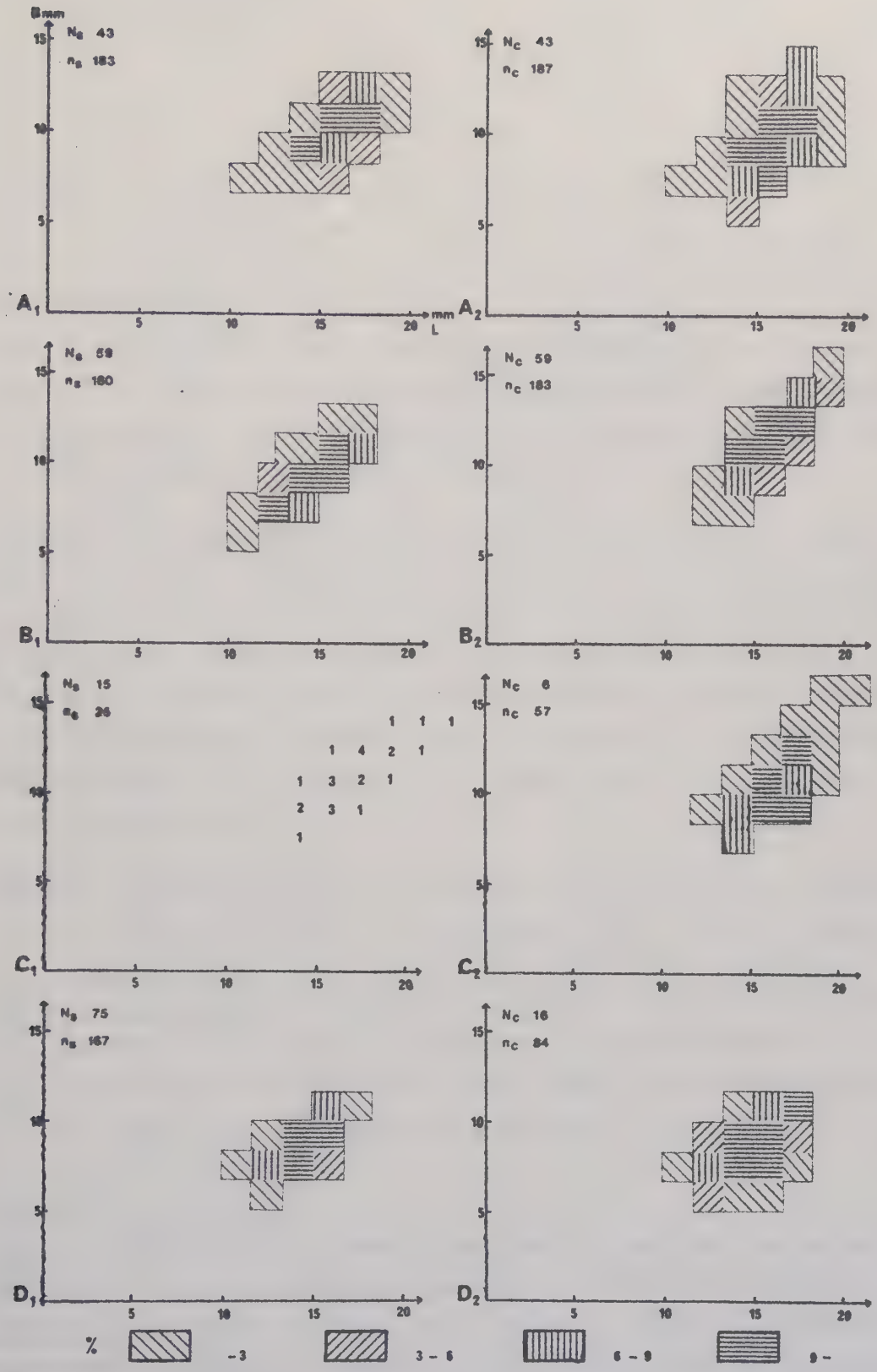


Fig. 38. Length (horizontal axis) and breadth of standards of herbarium material (left) and of cultivated material (right). Means of usually 5 measurements per plant. -- A: Lathyrus pratensis 2n=28. -- B: L. pratensis 2n=14. -- C: L. binatus. -- D: L. hallersteinii.

Obviously, diploids and in particular plants from the northern parts of Europe in such a cultivation (which is more favourable than in nature) got proportionally larger pollen grains than plants from other regions. A more suitable climate combined with a better supply of nourishment and water may be the reason for this increase (Fig. 42). However, the modificative variation in pollen diameter was considerably wider in Swedish than in German material (30 and 35 samples, respectively, were studied).

Tetraploid L. pratensis got larger pollen grains after 5 years cultivation, too. The variation was smaller in the French material in comparison with the studied material from other countries. In L. binatus the few cultivated plants examined showed small variation in pollen diameter between different years of cultivation In L. hallersteinii 34 plants after four years in cultivation had pollen grains on the average 2.5 μ longer than after one year in cultivation (Figs. 40, 42).

Biometric studies performed on herbarium material showed that the smallest pollen was found in L. binatus, while diploid L. pratensis and L. hallersteinii had about equally large pollen grains. Tetraploid L. pratensis had larger pollen grains than the others (Fig. 42). However, the overlapping was large in the material and it was not possible to decide from pollen grain size only whether, e. g. a plant of L. pratensis was diploid or tetraploid.

GYNOECIUM

About one half to two thirds of the bent up part of the carpel is papillose in the L. pratensis complex as in several species of Lathyrus (cf. Bässler 1973). Ovule number is often a good taxonomic character in Lathyrus (Hitchcock 1952). Taxa in the L. pratensis complex had about equal numbers of ovules, (6--) 10--12 (--14) (Fig. 44). In triploid L. pratensis no reduction of the ovule number was found.

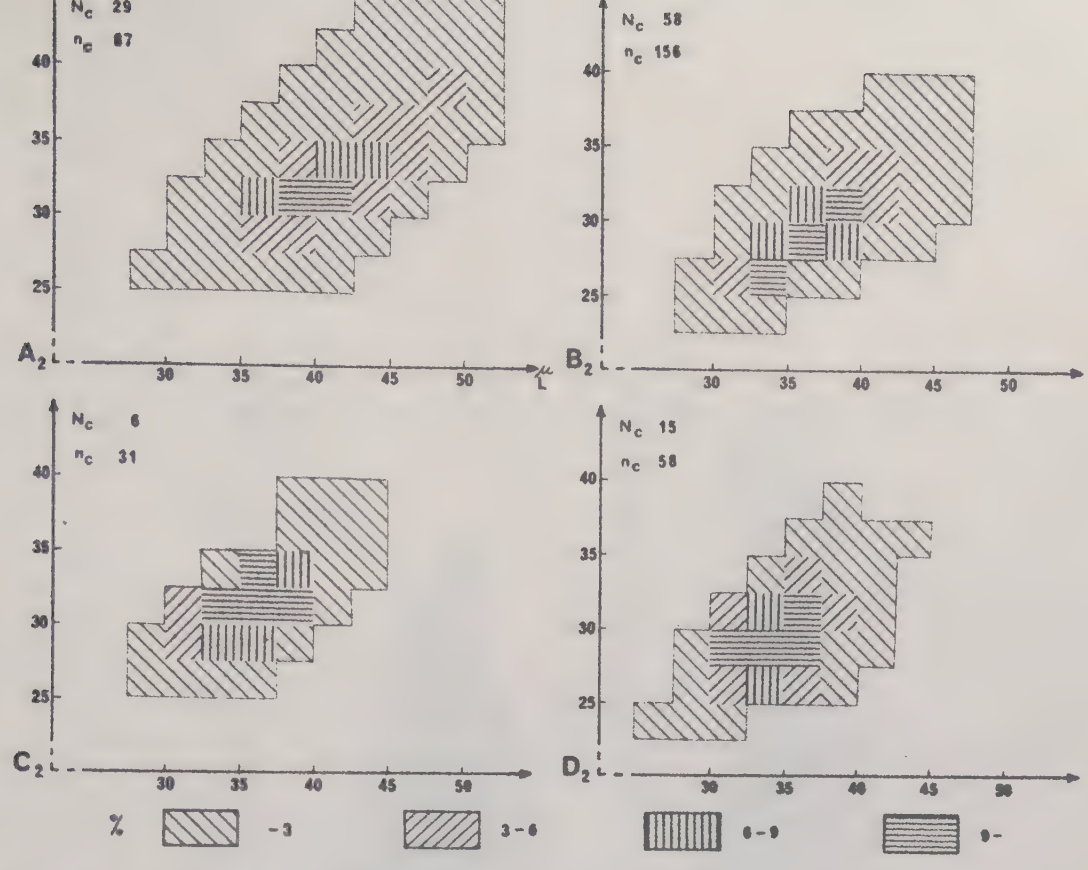


Fig. 39. Largest (l) and shortest (b) pollen diameter of cultivated material. Means of 10 measurements per plant. -- A: Lathyrus pratensis 2n=28. -- B: L. pratensis 2n=14. -- C: L. binatus. -- D: L. hallersteinii

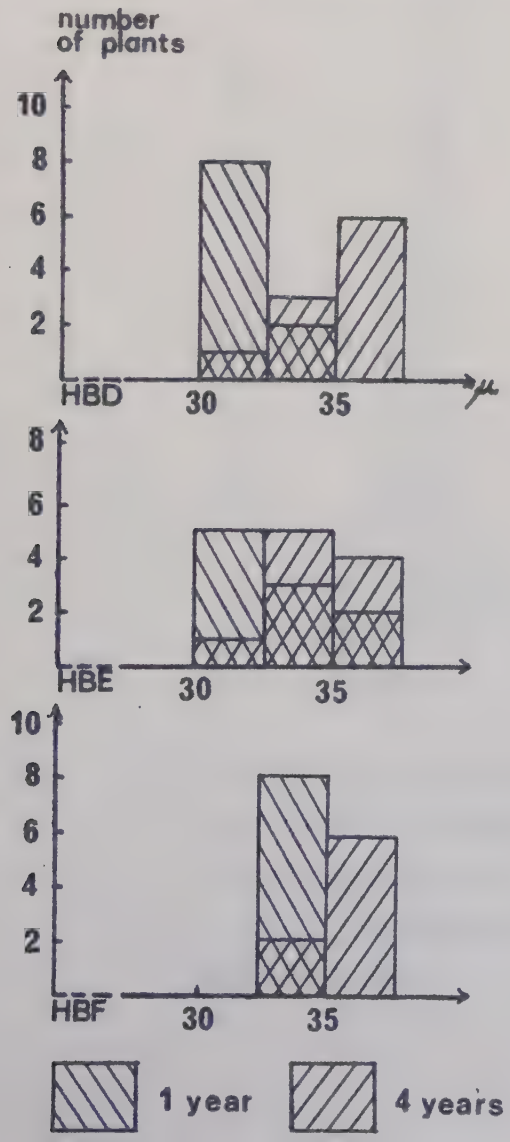
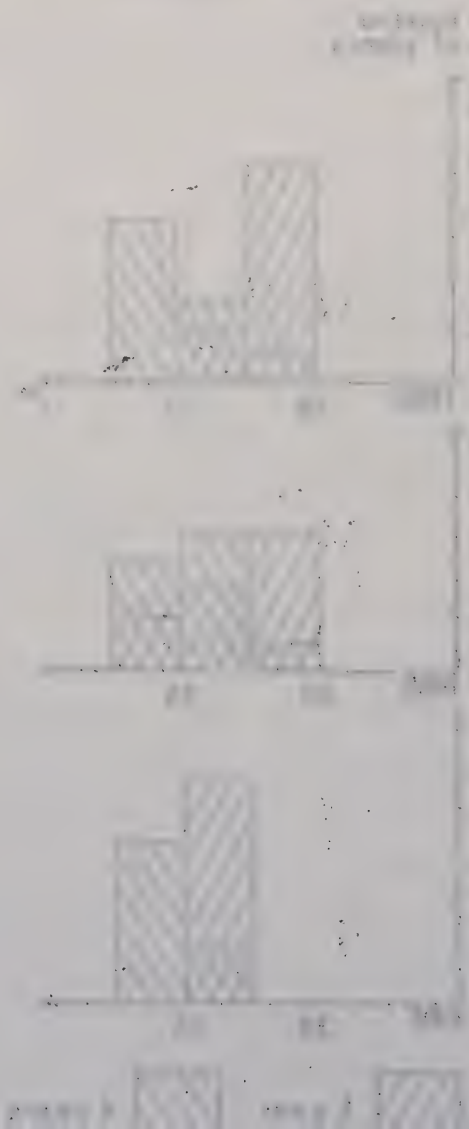


Fig. 40. Intrapopulational variation of pollen length in three samples of Lathyrus hallersteinii after one and four years in cultivation.



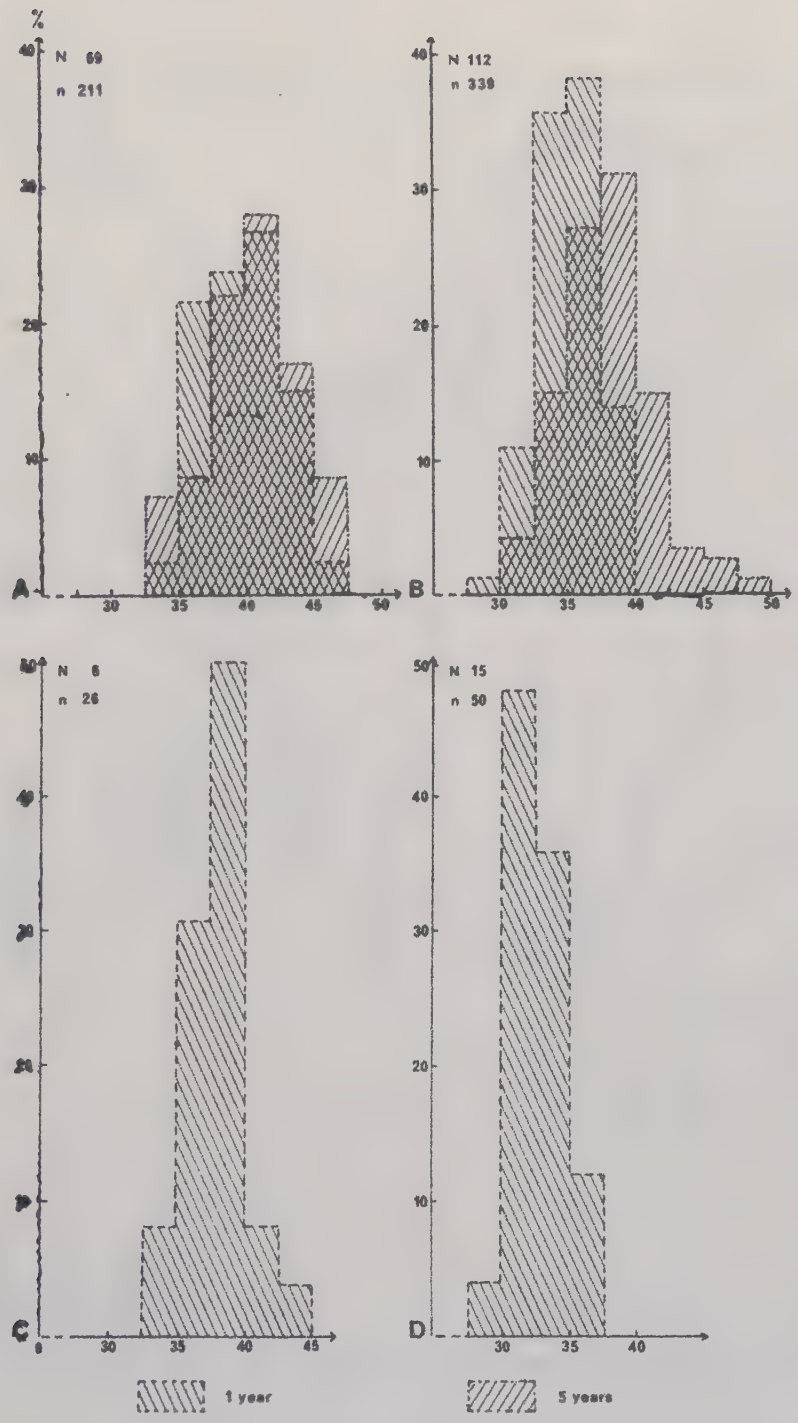


Fig. 41. Largest pollen diameter after one and after five years of comparative cultivation. Means of at least 10 measurements per plant. -- A: Lathyrus pratensis 2n=28. -- B: L. pratensis 2n=14. -- C: L. binatus. -- D: L. hallersteinii.

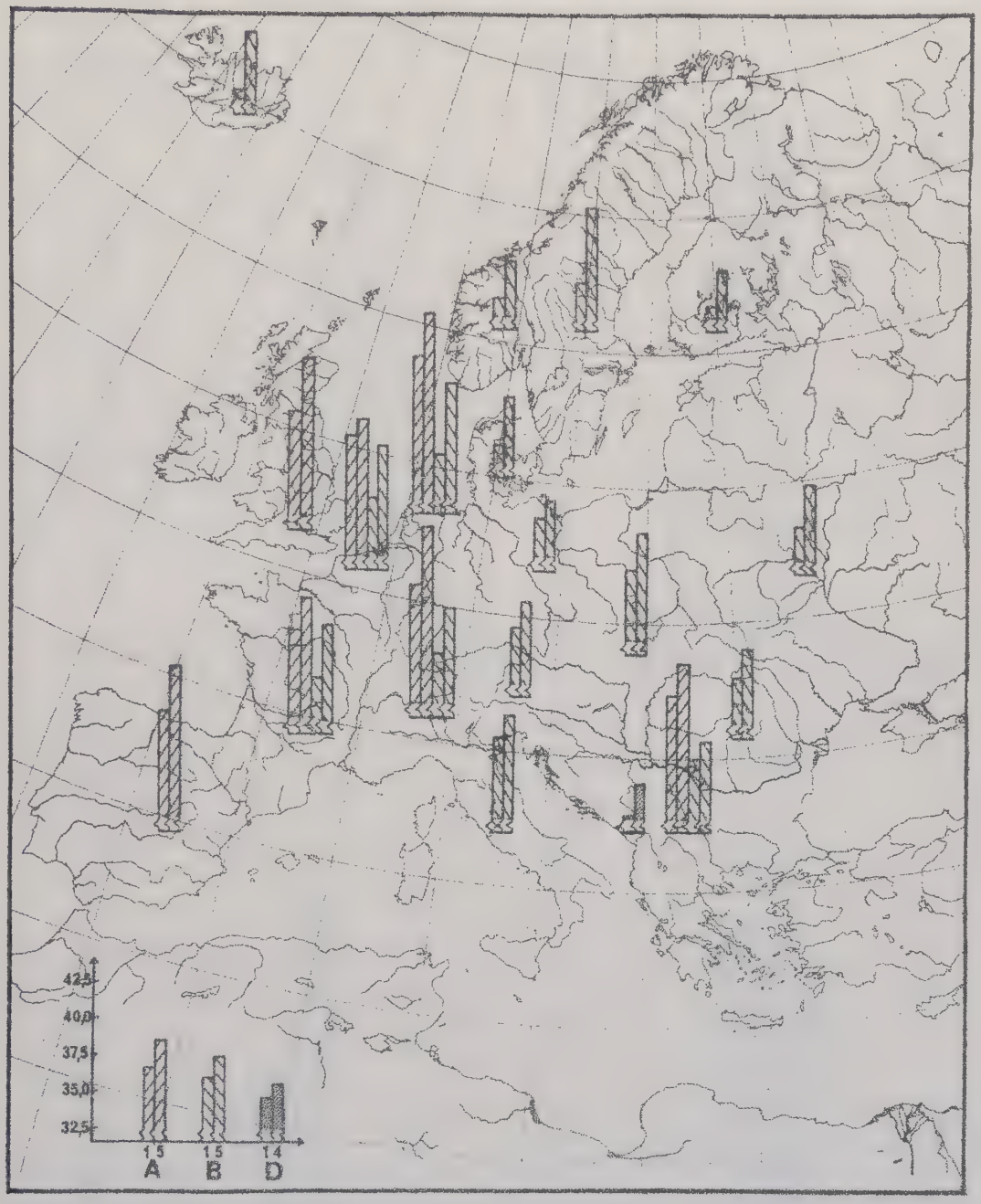


Fig. 42. Largest pollen diameter of cultivated Lathyrus pratensis 2n=28 (A), L. pratensis 2n=14 (B) and L. hallersteinii (D). Means of the studied samples from different countries, after one year (left) and after five (four) years (right) of cultivation. Means of at least 10 measurements per plant and 3 plants per population.

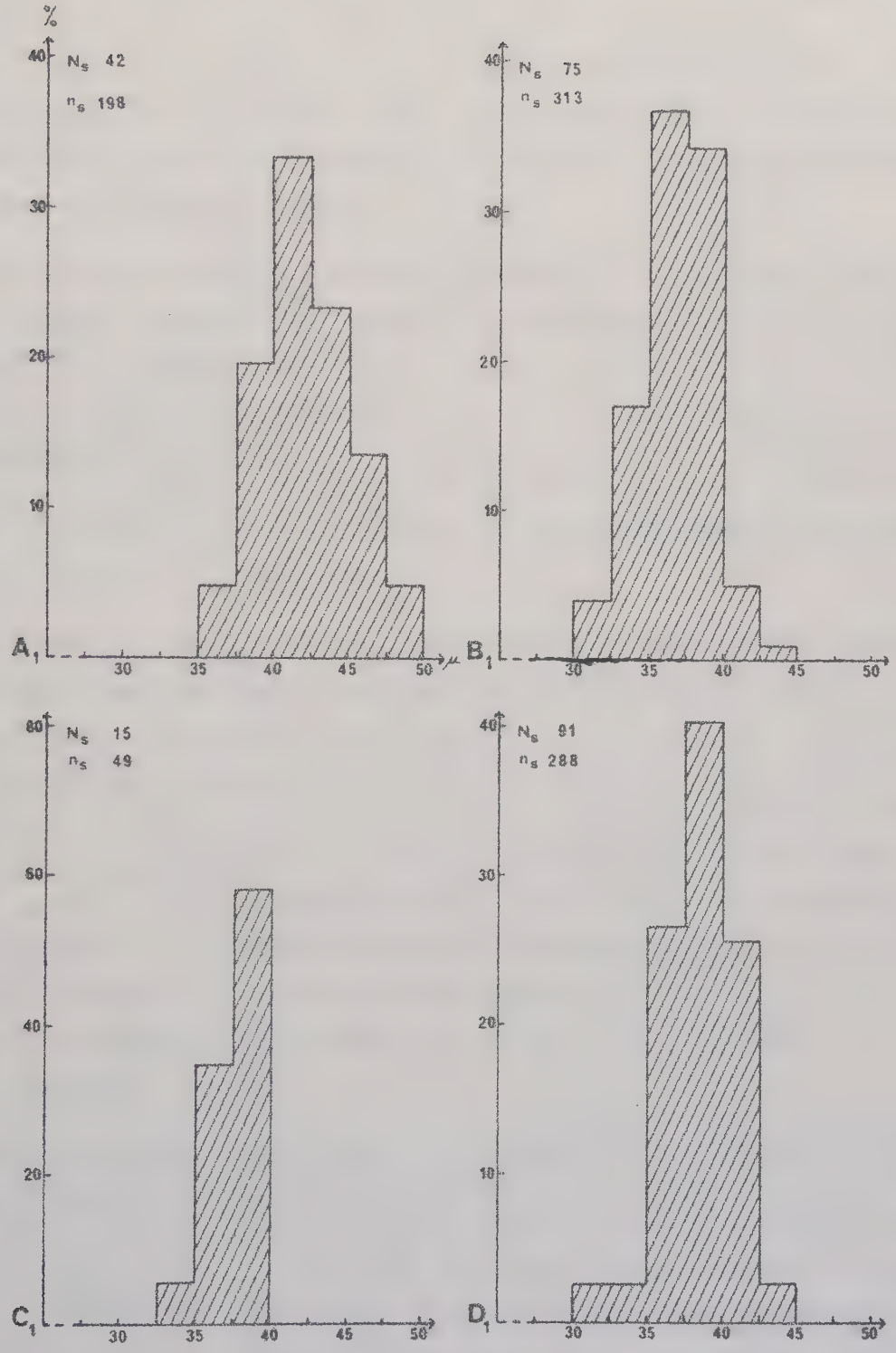


Fig. 43. Largest pollen diameter of herbarium material. Means of at least 10 measurements per plant. -- A: L. pratensis 2n=28. -- B: L. pratensis 2n=14. -- C: L. binatus. -- D: L. hallersteinii.

PODS AND SEEDS

The oblong-linear pods are 20--50 x 4--7 mm. No definite differences in size were found between taxa in the L. pratensis complex. The colour of the ripe legume is brown to blackish-brown. The upper suture is ± concave and the lower one straight to ± convex. The pod texture is obliquely nerved. In L. pratensis the pods were glabrous or sparsely pubescent. L. binatus and L. hallersteinii always had glabrous legumes.

The number of seeds per legume developed in nature was smaller in L. binatus (normally 1--3) and in L. hallersteinii (often 2--4) than in L. pratensis (commonly 3--6). The ± ellipsoid seeds were light green in L. hallersteinii and brown in L. binatus. In L. pratensis they varied from light green, violet to dark brown and were often spotted. The hilum of the seed was about 1/7--1/4 of the circumference. It was usually glabrous but pubescent in some populations of L. pratensis.

The size and the weight of the seeds are to some extent dependent on the number of seeds developed in the pod. However, when relatively many seeds of each collection are studied, this factor becomes less important and could be neglected in the comparison made. The weight of 100 well-developed seeds per sample in tetraploid L. pratensis (1100--1900 mg.) exceeded considerably that of the diploids (750-1650 mg., Fig. 45), though there was some overlapping. A certain correlation between weight and the largest diameter of the seeds (mean values 2.5--3.5 mm. at diploid level, 2.9--3.6 mm. at tetraploid level) of L. pratensis was found, as expected.

Only five seed samples each of L. binatus and L. hallersteinii were included in this investigation. The seeds of L. binatus were the largest ones in the complex. The mean values of the largest diameter were 3.4--4.1 mm. and the weight of 100 seeds 1400--1650 mg. The size and the weight of the seeds of L. hallersteinii (3.0--3.3 mm. in diameter, 1100--1500 mg. per 100 seeds) included in this investigation lay within the natural variation of diploid L. pratensis.

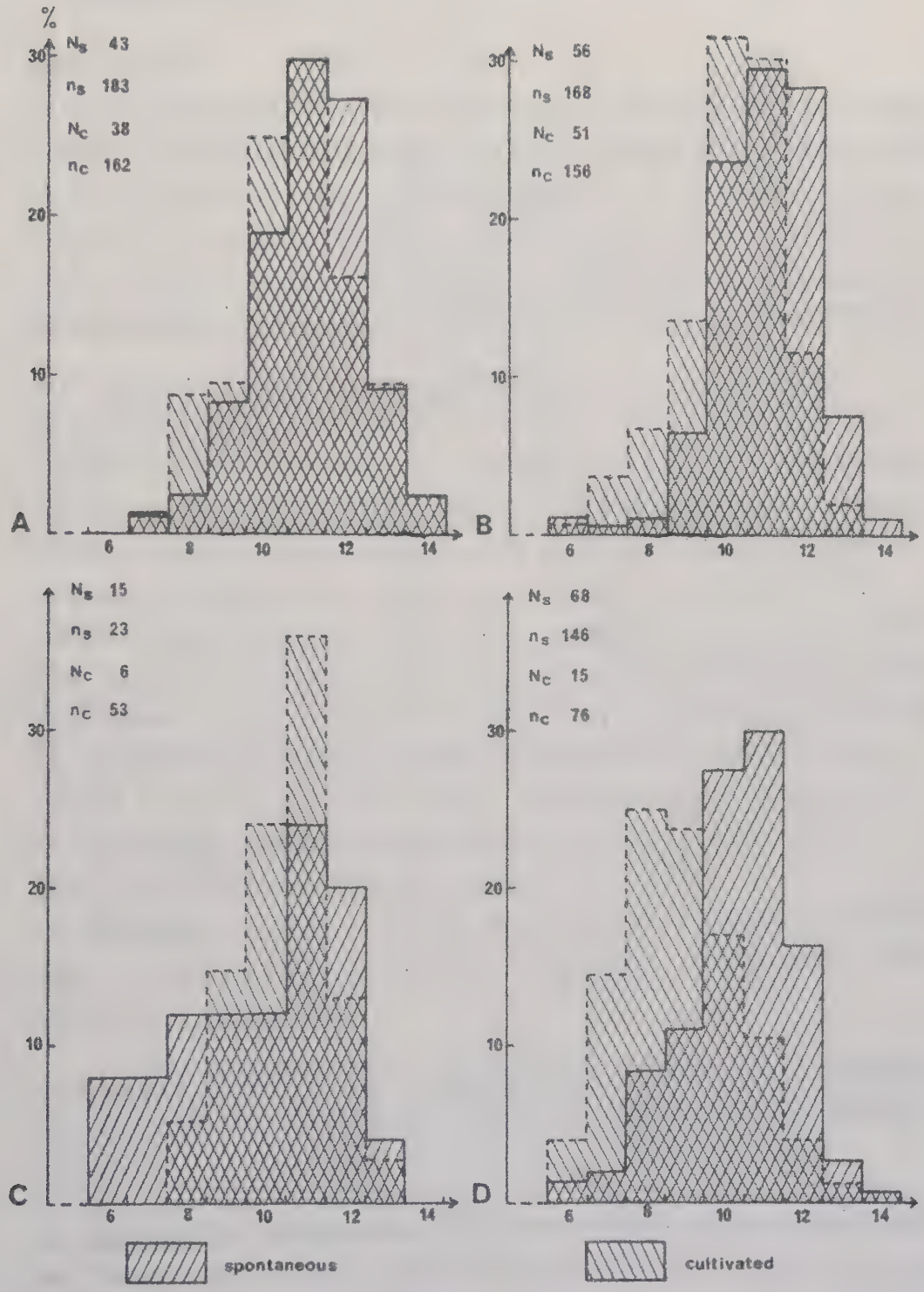


Fig. 44. Number of ovules per ovarium. Means of usually 3 counts per plant. -- A: Lathyrus pratensis 2n=28. -- B: L. pratensis 2n=14. -- C: L. binatus. -- D: L. hallersteinii.

The weight of seeds in the L. pratensis complex decreased from south towards north in Europe. This was most evident in diploid L. pratensis (Table 14).

CONCLUSIONS

In the L. pratensis complex the intraindividual and the intrapopulational variation were relatively small and confined mainly to the vegetative parts. The development of rhizomes, shoots, leaflets, stipules, stomata and pollen grains in a comparative study of diploid and tetraploid L. pratensis, L. binatus and L. hallersteinii was to some extent modified by the environment.

Diploid and tetraploid L. pratensis in Europe could not be morphologically distinguished. On the contrary, in most characters studied variation overlapped to a great extent and showed no discontinuity ascribed to chromosome number. However, average size of pollen grains and seeds was larger in the tetraploid than in the diploid material. No evident cline variation was found to occur in L. pratensis except that the seed in spontaneous material in the complex decreased in weight from south to north in Europe. Usually, in diploid as well as in tetraploid L. pratensis the flowers were larger at high levels e. g. in the Alps. Thus, the biometrical studies of L. pratensis, including material from a wide variety of biotypes in Europe, did not support a division of L. pratensis L. into specific nor subspecific taxa. Nevertheless, more detailed study may show e. g. certain ecologically correlated variation.

L. binatus Pančić , L. hallersteinii Baumg. and L. pratensis L. are possible to distinguish from each other on morphological grounds.

L. binatus is distinguished from the other two species by smaller total height, 10--25 cm, decumbent growth, ±glabrous shoots, unramified tendrils, smaller leaflets and stipules, (1--) 2--4 (--6) flowers per raceme, somewhat larger pollen grains and seeds, and glabrous legumes.

L. hallersteinii has 20--40 cm, ± erect and glabrous shoots, single

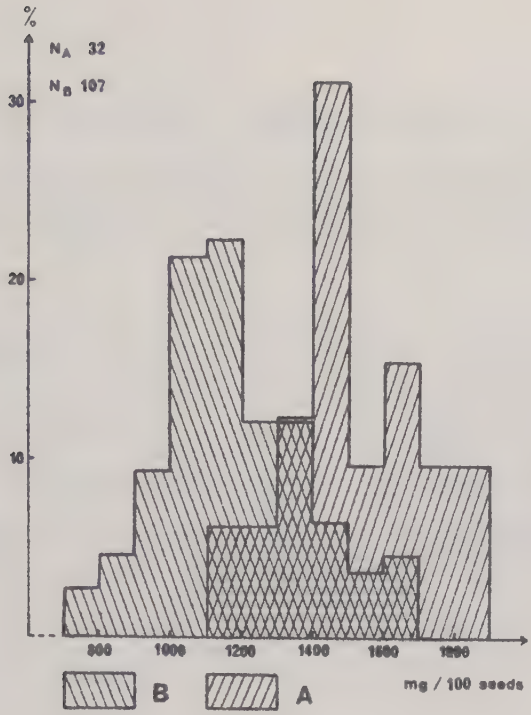


Fig. 45. Seed weight of spontaneous *Lathyrus pratensis*. -- A: 2n=28. -- B: 2n=14

Table 14. The seed weight after degree of latitude in spontaneous *Lathyrus pratensis* 2n=28 (32), *L. pratensis* 2n=14 (107), *L. binatus* 2n=14 (5) and *L. hallersteinii* 2n=14 (4). The weight in mg of 100 seeds per sample. Numbers of samples within parentheses.

Latitudes mg	700	800	900	1000	1100	1200	1300	1400	1500	1600	1700	1800	1900
L. pratensis 2n=28													
40° - 45°												1	
45° - 50°						1	1	1	5	2	3	2	1
50° - 55°						1	1	3	5	1	2		2
L. pratensis 2n=14													
40° - 45°						1	2	1	1		3		
45° - 50°				2	6	4	6	6	3	2	2		
50° - 55°		1	1	3	9	17	4	6	3	2			
55° - 60°			2	2	3	1	1						
60° - 65°		2	2	3	5	1							
L. binatus													
40° - 45°									1	2	2		
L. hallersteinii													
40° - 45°									2				
45° - 50°						1	1						

or ramified tendrils, larger leaflets and stipules, than the other species in the complex, (1--) 3--6 (--8) flowers in each of the unilateral racemes, calyx teeth of about equal length, and glabrous legumes.

L. pratensis has 30--90 cm tall, ± pubescent climbing shoots, often ramified tendrils, (1--) 5--10 (--13) flowers per raceme, the upper calyx teeth are much shorter than the lower, and the legumes are ± pubescent. The leaflets and the stipules are larger than in L. binatus but smaller than in L. hallersteinii.

XI TAXONOMY

The L. pratensis complex is a distinct and taxonomically well-delimited group that constitutes a separate section Pratensis Bässler of the genus Lathyrus within Leguminosae (Bässler 1966, p. 90, cf. p. 5). Five species have been described within the complex viz. L. pratensis L., L. sepium Scop, L. hallersteinii Baumg., L. lusseri Heer ex Kock, and L. binatus Pančić (chapter II). Below, morphological and biochemical characteristics in the complex are discussed as well as some different types of isolating mechanisms, that are of decisive importance in the process of speciation and in the evolutionary specialisation (divergence of evolutionary lines).

1. Genetic isolation

Four genetically isolated population groups can be distinguished: diploid L. pratensis, tetraploid L. pratensis, L. binatus and L. hallersteinii. No artificial hybrids between L. pratensis, L. binatus and L. hallersteinii were obtained in crossing experiments, nor have any been reported in nature.

Exceptionally, triploid sterile hybrids were obtained in crossing between diploid and tetraploid L. pratensis. Crossings within these four groups were successful with in most cases high fertility in F_1, including crosses between L. pratensis and sepium and lusseri-like material.

2. Morphology

Three morphologically clearly distinguishable population groups can be separated, viz. L. pratensis (diploids and tetraploids), L. binatus and L. hallersteinii. L. pratensis is extremely variable, while L. hallersteinii and L. binatus show a more or less restricted variation, particularly the last-mentioned group. The specific status of the groups is based largely on discontinuities rather than large differences in morphological characteristics (cf. Figs. 28--44). On morphological grounds and with respect to the size of the intra- and interpopulational variation, both L. sepium and L. lusseri are here included in L. pratensis.

In the present study, biometrical studies have not supported a division of L. pratensis (chapter X). Moreover, in modern plant taxonomy there is a general tendency not to give formal taxonomic separation at least below the rank of subspecies (cf. Huxley 1938, Runemark 1961, Nordborg 1967, Björkqvist 1968). Instead, L. pratensis at different ploidy levels are brought together, contrary to e.g. Löve & Löve (1956).

3. Biochemical characteristics

L. pratensis is distinguished from other Lathyrus species by having a quite remarkable flavonoid composition, for the leaves contain the very rare flavone tricetin and the yellow flowers, the flavonol syringetin, which according to Harborne (1971) is unique to this species. No reports about these compounds are given for L. binatus and L. hallersteinii.

Biochemical examinations of phenolic compounds in leaves of samples studied in the L. pratensis complex (Brunsberg 1965) showed some differences, e.g. delphinidin occurred in L. pratensis but was not found either in L. binatus or in L. hallersteinii. In the same manner they had other different compounds (Brunsberg 1965, p. 387). Besides, the amount of quercetin was much larger in the samples of L. binatus and L. hallersteinii analysed compared with L. pratensis. No differences in chemical compounds were registered at different ploidy levels of L. pratensis. The biochemical studies support a division of the L. pratensis complex into three groups.

4. Geographical and ecological separation

L. pratensis occurs over all Europe but also in North Africa and temperate Asia, and has been introduced into North America. Tetraploid L. pratensis was in the present study restricted to western and central Europe. In the westernmost parts (Great Britain, western France, Spain) it may be the only cytotype, while in other areas (e.g. the Netherlands, Belgium, eastern parts of France, the Alps at higher altitudes) diploid and tetraploid populations are allopatric.

L. binatus is only found in a small mountain area in Yugoslavia. L. hallersteinii is restricted to Roumania and Yugoslavia, possibly with out post localities in Hungary, Poland and Greece. Thus, L. binatus and L. hallersteinii are allopatric, while diploid L. pratensis is sympatric with both of them.

L. pratensis, L. binatus and L. hallersteinii are to a great degree ecologically separated (p. 56--66). L. binatus occurs mainly on exposed scree slopes on calcareous ground with sparse vegetation. L. hallersteinii prefers shadow, growing within oak-forests often with a well-developed bush-layer vegetation but with a sparse vegetation in the field-layer, while L. pratensis has a wider ecological preference and mainly grows on exposed localities, often in close vegetation.

5. Reproductive barriers

No general differences in reproductive system were found in the complex. All taxa display vigorous vegetative reproduction combined with somewhat reduced seed-setting (rarely more than 30 % of the flowers give ripe seeds). Within the complex incomplete barriers to selfing were found, that may vary in strength between populations, but that have genetic importance in species differentiation (cf. p. 30--36, 43--45). More studies of mechanical barriers in the reproduction, such as failure or ineffectiveness of pollen-tube growth and of the systems of compatibility and incompatibility compared with phytochemical investigations of taxa in the L. pratensis complex, would be of value in the elucidation of the evolution in the complex and within the whole genus. According to Simola (1967) it may be possible that some uncommon amino acids depending on content or not can promote or depress the growth of the pollen tubes of a plant and this phenomenon can explain the low proportion of hybridization of Lathyrus species. Lathyrus species that can ba crossed, are always chemically related (Bell & Fowden 1964, Simola 1966).

In flowering time, L. binatus and L. hallersteinii (mid-May--mid-June) are partially seasonally isolated from L. pratensis (about mid-June--mid-August).

TREATMENT

The following descriptions are based on spontaneous material.

Sect. Pratensis Bässler
Bässler 1966, p. 90.

Perennial, eglandular herbs. -- Rhizomes of varying length, often well-developed. -- Shoots 10-100 cm, stems angled to terete, procumbent to erect. -- Leaves tendrillous or aristate. -- Leaflets 1-paired, elliptic to lanceolate, parallell-veined from the base. -- Stipules large ± unequally sagittate, usually broader than the acute leaflets. -- Stomata on both surfaces of leaflets, epidermal cells with undulating walls. -- Plastids 10--15 (--25) per guard cell. -- Flowers in axillary few- to many-flowered racemes. -- Peduncle longer than the leaf. -- Bracts and bracteoles 1 x 1--4 mm, sometimes lacking. -- Pedicels 2--5 mm long. -- Calyx bilabiate, pubescent--glabrous, calyx teeth acuminate, unequal to ± equal in length, equal to or longer than the tube. -- Corolla yellow, standard bent upwards about right angles to wings and keel, wings free from the keel. -- Stamens diadelphous, the tube of the 9 united filaments truncate at apex. -- Pollen grains tricolporate, ellipsoid with no distinctive wall structure. -- Style bent upwards from ovary at various angles, neither twisted nor dilated above, about one half to two thirds bent up and papillose. -- Legumes oblong-linear, 20--50 x 4--7 mm, compressed, brown to blackish-brown, glabrous or hairy oblique-nerved; upper suture wingless, ± concave, lower suture straight to ± convex. -- Number of ovules (5--)10--12(--14). -- Seeds ± ellipsoid, light green, violet to dark brown, often spotted, smooth; hilum 1/7--1/4 of the circumference. -- Chromosome numbers 2n=14, (21), 28, (42).

Key to the taxa

1. ± Decumbent, 10--25 cm. Leaves mucronate or ending in a very short simple tendril. Raceme (1--)2--4(--6)-flowered , . L. binatus
1. Erect, ± climbing taller than 20 cm. Upper leaves at least ending in a distinct tendril 2
2. Raceme unilateral, (1--)3--6(--8)-flowered Calyx teeth ± equal in length. Shoot glabrous . . . . . L. hallersteinii
2. Raceme not unilateral, (1--)5--10(--13)-flowered. Calyx teeth unequal in length. Shoot pubescent--glabrous . . L. pratensis

Lathyrus pratensis L.

Linnaeus 1753, p. 733. -- Orobus pratensis (L.) Döll 1843, p. 787. -- Orig. coll. "Habitat in Europe pratis" (Linn 905/18, microfiche seen).

L. sepium Scopoli 1772, p. 64. -- L. pratensis L. var. sepium (Scop.) Grisebach & Schenk 1852, p. 294 (nomen, non planta). -- Orig. coll. "Habitat ad sepes agri Goriziences" (no authentic material has been traced).

L. lusseri Heer ex Koch 1845, p. 1066--1067 (non rite publ.).

ILLUSTRATIONS AND DIAGRAMS. Fig. 1 (habit), Figs. 29--45 morphological variation), Figs. 8--10 (cytology), Figs. 14, 16 (male fertility), Figs. 3, 4, 6, 19-22 (distribution), Fig. 23 (habitat).

Shoots (30--)50--90 cm long, erect, ± climbing pubescent--glabrous. -- Leaflets (6--)12--35(--45) x 1,5--9(--12) mm, linear-lanceolate to lanceolate or elliptical with simple or divided tendrils. -- Stipules (3--)5--27(--33) x 1,5--9(12) mm, linear to lanceolate, rarely ovate, shorter than or about as long as the leaflets. -- Stomata length (22--)25--35(--38) µ. -- Racemes not unilateral, (1--)5--10(--13)-flowered. -- Flower length (10--)12--18 mm. -- Calyx ± pubescent, calyx teeth unequal,

distance between the two upper shortest teeth about equal to their length. -- Corolla yellow, often with violet-coloured veins. -- Standard (10--)12--18(--20) x (5--)6--12(--14) mm. -- Pollen length in tetraploids (32--)37--47(--50) µ, in diploids (30--)32--40(--45) µ. Male fertility high in the diploids somewhat reduced in the tetraploids. -- Seeds commonly 3--6 per legume, tetraploid seeds 2,8--3,6 mm long, diploid seeds 2,5--3,5 mm long, weight of 100 seeds of the tetraploids 1100--1900 mg and in diploids 750--1650 mg, weight decreasing from south to north in Europe. -- Chromosome numbers 2n=14,(21),28(42).

FLOWERING PERIOD. June--August (--September).

DISTRIBUTION. All Europe, although more rare in the most southern and northern parts, North Africa and temperate Asia and introduced in North America. L. pratensis is classed among the West-European --South-Siberian plant group according to Hultén (1971). Tetraploid L. pratensis seems to be restricted to western and central Europe. Diploid L. pratensis has a wider and complementary distribution in Europe. In a zone through the Netherlands, Belgium, France and the Alps the cytotypes are sympatric.

HABITAT. Both diploid and tetraploid L. pratensis have a very wide ecological amplitude, often occurring in close vegetation in exposed localities. The cytotypes are common in e.g. tall-herb and dry-meadow vegetation as well as in vegetation of forest skirts, shores, banks and roadsides and in different kinds of soils, e.g. clay, lime, mould, moraines, sand etc.

Lathyrus binatus Pančić

Pančić 1874, p. 256. -- Orobus pratensis var. binatus (Pančić) Ascherson & Kanitz 1877, p. 106. -- L. pratensis var. binatus (Pančić) Hayek 1924--1927, p. 256. -- Orig. coll. Mokre Gore (no authentic material has been traced). -- Neotype: Serbia austr. occ. Mokra Gora in rupestris aridis. Bornmüller 27.VIII 1887 (PRC).

ILLUSTRATIONS AND DIAGRAMS. Fig. 1 (habit), Figs. 29--33,35--40,41-44 (morphological variation), Fig. 8 (cytology), Fig. 14 (male fertility), Fig. 5 (distribution), Fig. 24 (habitat).

Shoots 10--25 cm, ± decumbent, glabrous to almost glabrous. -- Leaflets 6--18(--24) x 1,5--6 mm, lanceolate with or without a very short simple tendril. -- Stipules 6--15(--18) x 1--6 mm, linear-lanceolate to lanceolate, shorter than or about as long as the leaflets. -- Stomata length 22-33 µ. -- Racemes (1--)2--4 (--6)-flowered. -- Flower length 13-22 mm. -- Calyx glabrous to almost glabrous, calyx teeth ± unequal in length, distance between the two upper shortest teeth equal to or shorter than their length. -- Corolla light yellow, without violet veins. -- Standard 14-22 x 7--15 mm. -- Pollen length (32--)35--40 µ. Male fertility in some individuals reduced. -- Seeds usually 1--3 per legume, seed length 3,4--4,1 mm, weight of 100 seeds 1400-1700 mg. -- Chromosome number 2n=14.

FLOWERING PERIOD. Mid-May--mid-June.

DISTRIBUTION. Yugoslavia (Bosna, Serbia).

HABITAT. On exposed scree slopes on calcareous ground with sparse vegetation. Often L. binatus grows in the protection of tussocks of Bromus on levels up to 1800 m.

Lathyrus hallersteinii Baumg.

Baumgarten 1816, p. 333--334. -- L. pratensis Hallersteinii (Baumg.) Reichenbach 1830--1832, p. 535. -- Orobus pratensis (L.) Döll var. Hallersteinii (Baumg.) Ascherson & Kanitz 1877, p. 106. -- Orig. coll. "Lathyrus sepium Scop. Transsilvania, Czora Majo 129" Baumgarten (W, lectotype).

ILLUSTRATIONS AND DIAGRAMS. Fig. 1 (habit), Figs. 29--44 morphological variation), Fig. 8 (cytology), Fig. 14 (male fertility), Fig. 5 (distribution), Fig. 23 (habitat).

Shoots 20--40(--50) cm, erect, glabrous. -- Leaflets (15--) 24--45(--57) x (3--)6--15(--18) mm, ovate with simple or divided

tendrils. -- Stipules (12--)18--36(--48) x (3--)6--15(--18) mm, ovate, equalling to larger than leaflets. -- Stomata length (20--)22--30(-33) µ. -- Racemes unilateral (1--)3--6(--8)-flowered. -- Flower length (9--)11-14(--16) mm. -- Calyx glabrous, calyx teeth ± equal in length. Distance between the two upper teeth less than their length. -- Corolla yellow, rarely with violet-coloured veins. -- Standard (10--)12--16(--18) x (5--)6--12 mm. -- Pollen length (30--) 35--42(--45) µ. Male fertility very high. -- Seeds usually 2--4 per legume, seed length, 3,0--3,3 mm; weight of 100 seeds 1100-1500 mg; weight of the seeds decreasing from south to north in Europe. -- Chromosome number 2n=14.

FLOWERING PERIOD. Mid-May--mid-June.

DISTRIBUTION. Roumania and Yugoslavia, possibly with out post localities in Hungary, Poland and Greece.

HABITAT. In shadow within oakforests with a sparse vegetation in the field-layer and with a well-developed bush-layer vegetation.

XII THE PROBLEM OF AUTOPOLYPLOIDY

The definition of autopolyploidy, originally in the sense of the doubling of one and the same chromosome set (Kihara & Ono 1926), has gradually become more distinct (e.g. Darlington 1932, Müntzing 1936, Clausen, Keck & Hiesey 1945, Stebbins 1947, 1950, Grant 1971). Between strict autopolyploids, that are nonhybrids arisen from one individual or one population, to interracial autopolyploids, segmental allopolyploids, over to the extreme contrast, genomic allopolyploids, that are hybrids between species at polyploid level, there is a graded series. Interracial autopolyploids are developed from diploid forms which may differ morphologically from each other and have different geographical distribution or ecological preferences, but which form fertile hybrids at diploid level. Segmental allopolyploids are characterised by such differences in the chromosome segments whereby different genomes produce sterility at diploid level. Strict autopolyploids and racial autupolyploids have often been confused with segmental allopolyploids by some similarities, e.g. in chromosomal behaviour in meiosis, morphological resemblance etc.

Most spontaneous polyploids are now considered to be of allopolyploid origin, viz. polyploidy in nature is nearly always associated with hybridization, either intervarietal or interspecific. In a survey of natural polyploids of thoroughly investigated plant groups Galax aphylla, Biscutella laevigata and Zea pereniis have been classified as autopolyploids (Clausen, Keck & Hiesey 1945). In addition, Vaccinium uliginosum, Eragrostis pallescense and Galium mollugo as well as G. verum have been mentioned as probable autopolyploids. In a critcal review including these examples Stebbins (1947) stated that the only clear-cut autopolyploid was Galax aphylla. Strict autopolyploidy is at present proved only in Vaccinium uliginosum by a reinvestigation (Rousi 1967) and in Epilobium angustifolium (Mosquin 1971) on cytogenetic evidence where interracial autopolyploidy has been shown in Biscutella laevigata and Solanum tuberosum.

The following four principal criteria have been used to distinguish typical autopolyploids from allopolyploids: chromosome behaviour (particularly the presence or absence of multivalents at meiosis), fertility, tetrasomic segregation, and the degree of morphological resemblance (Stebbins 1950, Grant 1971). However, it is difficult to identify naturally occurring polyploids as autopolyploids or allopolyploids. Only by taking all the criteria mentioned above into consideration and by experimentally resynthesising the polyploid from its putative ancestors in the complex studied, it is possible to identify its nature and origin in a satisfactory manner.

AUTOPOLYPLOIDY IN LATHYRUS PRATENSIS

From the present study of L. pratensis the following indications of autopolyploidy may be listed.

(1) The male fertility, expressed as the percentage of stainable pollen, was in the present study reduced to some extent at tetraploid level of L. pratensis in comparison to the diploids (p. 39, Fig. 14). Studies of male fertility in investigations of the frequency of pollen germination on agar medium (Figs. 15, 16) showed more evident and differentiated results (Fig. 14, p. 41, 43), viz. usually 70--100 % in the diploids and 40--100 % in the spontaneous tetraploids. The pollen fertility in the artificial tetraploids was lower than in the spontaneous tetraploids but higher than in the parental triploid. The pollen germination of the triploids was low (as a rule less than 10 %, but in a few cases up to 30 %).

(2) Studies of meiosis in euploids showed that the number of irregularities in spontaneous tetraploids increased considerably compared to diploid level (Table 4). Disturbances were found in all of the seven tetraploid plants from six samples examined as

opposed to two plants from ten populations at diploid level. In diploids and tetraploids 0,4 % and 37,7 % respectively of all cells studied showed disturbed meiosis (Table 4). At diploid level bivalent formation was normal (99,7 %). The formation of up to four quadrivalents in one single cell at metaphase I in spontaneous tetraploid L. pratensis was found (Table 5). As many as 44 % of the chromosomes of the cells studied formed multivalents at tetraploid level (Table 5). The high multivalent formation in the tetraploids indicates a high degree of homology between genomes and chromosomes and that the genomes are hardly of alloploid origin. This fact is a clear criterion of autopolyploidy in L. pratensis. Besides, the occurrence of unreduced gamets (Fig. 10:J) points to the possibility of autopolyploidy to arise in L. pratensis. Irregular division at meiosis (Fig. 10) and production of gamets with abnormal chromosome combinations can partly explain the reduced male fertility at tetraploid level compared to at diploid level. However, it is uncertain whether there is any correlation between the degree of gamete sterility in L. pratensis and the amount of uneven segregation of homologous chromosomes from a multivalent, as the segregation can partly be genetically determined. In this respect there might be differences between populations, too.

In spontaneous triploid L. pratensis as many as five trivalents in one single cell were found. About 45 % of the chromosomes formed trivalents and only 30 % bivalents (Table 5). The chromosomal behaviour indicates that the plants are probably autotriploids.

(3) There was close agreement in chromosome morphology between the few karyotypes studied at different ploidy levels. The karyotypes of all taxa studied within the complex were structurally similar.

(4) Comprehensive biosystematic studies of the genetic and modificative variation in morphological characters within the

L. pratensis complex showed great morphological resemblance at different polyploid levels of L. pratensis -- a principle criterium of typical autopolyploids. In fact, it was impossible morphologically to distinguish diploid and tetraploid L. pratensis while there were distinct morphological differences to the closely related taxa binatus and hallersteinii (Figs. 29--45). The variation of most characters studied of diploid and tetraploid L. pratensis overlapped to a great extent and showed no discontinuity ascribed to chromosome number. The size of individual cells (stomata, pollen) increased to some extent at tetraploid level compared to diploid level, but there was also modificative variation (Figs. 32, 41--43) in addition to the genetic differences. The individual organs and the plant as a whole changed very little with polyploidy in spontaneous L. pratensis. For instance, the size of the flowers, previously used in taxonomic separation of diploid and tetraploid L. pratensis, showed similar variation of the two cytotypes e.g. in the Alps. Indeed, it was impossible to distinguish diploids and tetraploids according to floral size. However, at tetraploid level the size as well as the weight of the seeds were larger (Table 14, Fig. 45). The small degree of gigas effects seems to be a factor indicating good ability to survive in nature.

(5) Analyses of phenolic compounds in leaves of European L. pratensis by thin-layer chromatography showed some interpopulational variation, but no recognisable differences were found between diploid and tetraploid L. pratensis, as distinguished from the other taxa studied in the complex (Brunsberg 1965). More comprehensive studies including more extensive material and studies of more chemical compounds (unpublished) by the author support these results.

(6) The breeding system with autogamy as well as allogamy (p. 45) in both diploids and tetraploids (autogamy is favoured when pollen from other individuals are put on the stigma) and a certain pollen fertility in spontaneous triploids may greatly extent the chances of getting successful natural autopolyploids. However, the genetic systems of compatibility and sterility are unknown in the complex.

(7) The plants are perennial and have a good vegetative proliferation by rhizomes (p. 48) -- factors of great importance in the survival of newly arisen polyploids. This is exemplified in the present study by a spontaneous triploid population with a vigorous vegetative development studied for 15 years.

(8) Ecological observations of the author's own collections of spontaneous material in the present study from most countries in Europe have not revealed any obvious differences between different ploidy levels of L. pratensis, while clear ecological preferences of respectice pratensis, binatus and hallersteinii within the complex were found (Table 13, Figs. 23--25).

(9) Artificial tetraploids produced from spontaneous triploid L. pratensis, collected in Sweden where otherwise only diploids have been found, showed great morphological resemblance to the parent. Relatively small development of gigas forms, mainly in individual cells, e.g. stomata and pollen, occurred, but the leaflets and the stipules were also somewhat larger than those of the parental triploid as well as of spontaneous tetraploids (Figs. 18, 29, 30, 32, 41). The two hexaploid plants found in the present study were less vigorous and did not flower; they had obviously exceeded the optimum development that in L. pratensis lies at diploid as well as at tetraploid level.

The pollen fertilify of the artificial tetraploids varied but was relatively high, probably depending on unexpectedly high pollen function of the parental triploid (Fig. 14). The artificial autotetraploids showed disturbances at meiosis as spontaneous tetraploids. A few crosses done between artificial and spontaneous tetraploids were successful.

CONCLUSIONS

The possible occurrence of unreduced gametes; the existence of spontaneous autotriploids in North Europe; resynthesising of tetraploids that were of a similar appearance as spontaneous tetraploids; high multivalent formation in meiosis and reduced male fertility of spontaneous tetraploid L. pratensis compared with at diploid level; and the high degree of morphological

resemblance and the similarity of composition of chemical components at different ploidy levels are all facts that, according to the present author, clearly indicate strict autopolyploidy in L. pratensis. Besides, there is the possibility of existing spontaneous chromosome doubling in vegetative tissue.

Finally, the partly separated geographical distribution of diploid and tetraploid L. pratensis in Europe may depend on that the tetraploids by partially different morphological and physiological features (e.g. larger stomata and pollen, slower growth with more intensive flowering period later in summer and delayed seed-setting) are better adaptive in the more warm and humid climate in the westermost parts of Europe compared to the diploids (cf. Epilobium angustifolium, Mosquin 1967).

Whether the polyploids of L. pratensis have a multiple origin from various regional diploids is not known for the present. However, this is more probable than a monophyletic origin followed by a gradual differentiation, in particular as the diploids and tetraploids have a very similar breadth of variation of different characters.

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APPENDIX I

LOCALITIES OF CULTIVATED SPONTANEOUS MATERIAL

Code

Each collection was designated by means of a combination of letters denoting the locality and a number denoting the plant, e. g. PAA:2. For *L. pratensis* the initial letter is P, for *L. binatus* B and for *L. hallersteinii* H. The second letter denotes geographic origin as follows:

Designation	Origin
L. pratensis	
PA	Finland, Iceland, Norway
PB	Sweden
PC	Sweden
PD	Sweden
PE	Denmark
PF	Denmark
PG	Great Britain
PH	The Netherlands
PJ	Belgium
PK	Germany
PL	Germany
PM	Germany
PN	Czechoslovakia
PO	Hungary, Poland, USSR
PP	France
PQ	France
PR	Switzerland
PS	Switzerland
PT	Austria
PU	Roumania, Spain
PV	Italy
PX	Yugoslavia
PY	Yugoslavia
L. binatus	
BA	Yugoslavia
L. hallersteinii	
HA	Roumania
HB	Yugoslavia

The third letter (where necessary, a fourth) is specific to each sample. The collections from each country are divided up according to province and are arranged in alphabetical order according to the locality. The spelling of geographical names is mainly according to Times Atlas (Bartholomew 1955--1956).

List of localities

Collection within parentheses. ^{x}Samples with plants drawn up from sponteneous seed material.

Lathyrus pratensis L.

AUSTRIA. 2n=14 K ä r n t e n. Kanzel, meadow 400 m (PTO). -- O b e r - Ö s t e r r e i c h. Altheim, meadow (PTD). -- Linz, 10 km W, roadside (PTE). -- Taufkirchen, roadside (PTC). -- S t e i e r m a r k. Altenmarkt, tall-herb meadow 400 m (PTG). -- Fürstenfeld, 2 km E, river bank (PTN). -- Graz, 5 km N, roadside (PTK). -- Haus in Ober-Ennstal, roadside (PTF^{x}). -- Leoben, 5 km E, tall-herb meadow (PTM). -- Präbihl, 900 m (PTH). -- Präbihl, in Pinus forest 1150 m (PTJ). -- Vordenberg, meadow 800 m (PTL). -- Vordenberg, edge of Picea wood 1050 m (PTQ). -- T i r o l. Brenner Pass, near the custom house, subalpine meadow 1300 m (PTB). -- Seefeld, wet meadow 1000 m (PTA).

2n=28 N i e d e r - Ö s t e r r e i c h. Gahn, south side of the mountain (PTP^{x}).

BELGIUM. 2n=14 A n t w e r p e n. Merksem, 1 km E, bank of small stream (PJA). -- L i é g e. Limborch (PJJ^{x}). -- W e s t - V l a n d e r n. Keeim, roadside (PJE). -- Nieuwmunster, bank of small stream (PJC). -- St Pieters Kapelle, bank of small stream (PJD). -- Smiske, roadside (PJF). -- Zuienkirke, 2 km S, bank of small stream (PJB).

2n=28 O o s t - V l a n d e r n. Ursel, 4 km W, roadside (PJG). -- W e s t - V l a n d e r n. Voormezele, bank of small stream (PJH).

CZECHOSLOVAKIA. 2n=14 B o h e m i a. Boreč near Lovosiae, meadow (PNC^{x}). -- Brdy, 550 m (PNG^{x}). -- Brdy, on limestone 300 m (PNX^{x}). -- Černolice, Řitka 450 m (PNA^{x}). -- Jininice (PNE^{x}). -- Karlštejn, wet meadow (PNF). -- Klánovice, edge of forest (PNJ^{x}). -- Krkonoše, 900 m (PNK^{x}). -- Mount Krkonoše, roadside (PNQ^{x}). -- Mount Lausitz, meadow on limestone 650 m (PNYA^{x}). -- Liblice near Český Brod, meadow (PNL^{x}). -- Lovos near Lovosiae (PNB). -- Milesovka, 750 m

(PND). -- Vodňany, Albrechtice (PNH^{x}). -- Vráž at Čakov, meadow (PNU^{x}). -- Vsenory, 250 m (PNM^{x}). -- Praha-Zäpad, Borek at Yelovè (PNV^{x}). -- M o r a v i a. Brno (PNYB^{x}). -- Jihlava, wet meadow (PNN). -- Karlovice (PNO). -- Modrice (PNP^{x}). -- S l o v a k i a e. Kremnica, Rembiz 600 m (PNYC^{x}). -- Kremnica, Kremnické 550 m (PNR^{x}). -- Kremnické, Kremnica-Rembiz, on andecite (PNYC^{x}). -- Malachy Inovec, Mala Lehota, river bank 520 m (PNS^{x}). -- Stredné Slovensko, Nová Baňa 200 m (PNT).

DENMARK. 2n=14 B o r n h o l m. Aarnager, sandy shore (PFE). -- Boderne, sandy shore (PFC). -- Hammershus, dry meadow (PFD). -- Risegaard, sandy shore (PFB). -- Svartingedal, tall-herb meadow (PFF). -- F y n. Bredstrup Mosse, wet meadow (PEQ). -- Uggerslev, edge of cultivated area (PER). -- J y l l a n d. Aarhus, Aabyhöj, river bank (PEH). -- Aaspe, 1 km S, wet meadow (PEO). -- Aggersund, 1 km S, bank of shell-rich gravel (PEF). -- Brovad, tall-herb meadow (PEK). -- Esbjerg, Tarp, 2 km SE, roadside (PEM). -- Esbjerg, Vong, bank of small stream (PEN). -- Fakkegrav, dry meadow on sand (PEJ). -- Krik, tall-herb meadow (PEC). -- Krik, roadside (PED). -- Lild K, wet meadow (PEA). -- Lindum, tall-herb meadow (PEG). -- Lönne K, 1 km S of church, bank of small stream (PEL). -- Tönder, tall-herb meadow (PEP). -- Voldum, inner dunes (PEB). -- Ydby, 3 km S, wet meadow (PEE). -- L o l l a n d. Fuglese, roadside (PES). -- M ö n. Möns klint, sandy slope 100 m (PEY). -- Möns klint, chalk cliffs 40 m (PFA). -- S j a e l l a n d. Hellested wet meadow (PEV). -- Jyderup, 2 km W, wet meadow (PET^{x}). -- Kalvehave, 2 km N, roadside (PEX). -- Ströby Ladeplads, roadside (PEU).

FINLAND. 2n=14. O u l u. Kempele (PAK^{x}). -- T u r k u. Ja Pori, Finby, Inkola, roadside (PAM). -- Nittymaa, Ulvila (PAL^{x}). -- Sumiaien (PAT). -- U u s i m a a. Artjärvi (PAQ^{x}). -- Kirkkonumm (PAS^{x}). -- Porvoo (PAR). -- Porvoo, Aunla, roadside (PAO^{x}). -- Porvoo, Suomentcyta (PAP^{x}). -- Porvoo, Suomenkylä (PAN^{x}).

FRANCE. 2n=14 A r d e n n e s. Carignan (PPK). -- Douzy, bank of small stream (PPJ). -- B a s - R h i n. Hipsheim, Ohnenheim (PJU^{x}). -- Plobsheim (PPN^{x}). -- C ô t e d'O r. Barges, meadow (PPY^{x}). -- H a u t e - S a v o i e. Annecy, 1 km E, dry slope on

limestone 470 m (PQN). -- Mont Salève, 1000 m (PQM^{X}). -- M e u r t h e - e t - M o s e l l e. Avril, dry meadow (PPM). -- M e u s e. Marville, dry meadow (PPD).

2n=28 A i s n e. La Capelle, 4 km E, roadside (PPG). -- A r d e n n e s. Maubert Fontaine, tall-herb meadow (PPH). -- A u d e. Roquetevil, 1000 m (PQU^{X}). -- C a l v a d o s. Caen, 3 km NE, bank of the Orne (PPP^{X}). -- Danvou (PPO^{X}). -- C a n t a l. Ytrac, 600 m (POJ^{X}). -- C h a r e n t e. Angoulème, 5 km SW, dry meadow (PQF). -- C h a r e n t e - M a r i t i m e. Angoulins-S-Meer, (PQD^{X}). -- C ô t e d' O r. Longvic, Marey-les-Fussey (PQT^{X}). -- Marcy syr Till, 400 m (PPV^{X}). -- Messigny, 320 m, roadside on limestone (PQYD^{X}). -- Moley, (PPU^{X}). -- Sainte-Isabelles, roadside (PPX^{X}). -- C ô t e s d u N o r d. Near Chacité, (PQK^{X}). -- Étables s/Mer, (PQYE^{X}). -- Plérin, (PQYF^{X}). -- D e u x - S è v r e s Le Mothe, St Héraye (PQE^{X}). -- D o u b s. Besançon, meadow on limestone 300 m (PQO^{X}). -- F i n i s t è r e. Morlaix, Plougonven (PQYJ). -- H a u t e s - A l p e s. Col du Lautaret, alpine meadow on a southerly slope 2200 m (PQS). -- H a u t e - G a r o n n e. Croix Falgarde (PQX). -- I s è r e. St Victor de Cessieu at La Tour du Pin, meadow 400 m (PQL^{X}). -- L a n d e s. Tarnos, 50 m (PQYA^{X}). -- L o i r e - I n f é r i e u r e. Bouée, (PQC^{X}). -- N o r d. Arleux, canal bank (PPD^{X}). -- Aubenchaeul-au-Bac, tall-herb meadow (PPC). -- Catillon, 2 km S, bank of small stream (PPF). -- La Cateau, 2 km NW, roadside (PPE). -- Douai near Scarpe, (PQYC^{X}). -- Lille, Asci (PQYH). -- Waasten, 1 km S, bank of small stream (PPB). -- P a r i s. Forêt de Marly, woodland (PPQ^{X}). -- Forêt de Sénart, woodland (PPR^{X}). -- P a s - d e - C a l a i s. Hesdin, (PQYB^{X}). -- Oisy-le-Verger, roadside (PPA^{X}). -- P u y - d u - D o m e. Le Breuil 400 m (PQH^{X}). -- St Hyre, 1000 m (PQG^{X}). -- P y r é n é e s - O r i e n t a l e s. Mont Louis, 1400 m (PQV^{X}). -- R h ô n e. Irigny, 10 km S of Lyon (PQB^{X}). -- S a v o i e. Col du Petit St Bernhard, alpine meadow, 1460 m (PQR). -- Bourg - St Maurice, 2 km SW, 850 m (PQP). -- Col du Petit St Bernhard, by a small stream 1160 m (PQQ). -- Termignon, 1350 m (PPS^{X}). -- S e i n e e t O i s e. Athis Mons, (PPT^{X}). -- V a u c l u s e. Mont Ventoux, Chapelle St. Basile, in a <u>Quercus</u> forest (PQA). -- V i c - s u r - S e i l l e. Moselle, (PQYG^{X}).

2n=42 P a r i s. Forêt de Senart, woodland (PPR^{x}).

GERMANY. 2n=14 B a d e n - W ü r t t e m b e r g. Au am Rhein, 3 km W, bank of the Rhine (PLU). -- Lahr, 10 km SW, bank of small stream (PLV). -- Lindau, Allgau, Simmerberg, meadow (PMF^{x}). -- Lindau, Allgau, Weiler (PME). -- Margentheim, Schirmback (PLT^{x}). -- Steig, tall-herb meadow, 800 m (PLY). -- Stühlingen, 5 km NE, roadside (PMB). -- Titisee, roadside (PLX). -- Tübingen, Pfaffingen, edge of forest 400 m (PMC^{x}). -- Wellerdingen, tall-herb meadow (PMA). -- Zwiefalten, dry meadow (PMD). -- B a y e r n. Barbing, 2 km ESE, dry meadow on sand (PLP). -- Bischofsheim, 10 km SE, dry meadow 500 m (PLJ). -- Bodensee, Krustanz (PLS^{x}). -- Breitengüssbach, 1 km NW, bank of Main (PLK). -- Denkendorf, roadside (PLN). -- Erlangen, 10 km S, in Pinus forest, 250 m (PLL). -- Hemau, 8 km N, the edge of cultivated area on sand, 530 m (PLO). -- Murnau, 3 km S, tall-herb meadow (PMG). -- Platting, dry meadow on sand (PLQ). -- Retzbach, roadside (PLM). -- Starnberg, 10 km NE, edge of Quercus forest (PLR). -- H e s s e n. Frankfurt am Main, Niederrad, bank of Main (PLG^{x}). -- Göttingen, Willershausen (PLE^{x}). -- Kassel, 5 km SE, roadside (PLH^{x}). -- Stoldt, (PMYB^{x}). -- Wetzlar, Lahn (PLF^{x}). -- N i e d e r s a c h s e n. Bad Harzburg, Bütterberg, on calcareous sand (PMX^{x}). -- Celle, 10 km S, roadside (PKS). -- Elmendorf, wet meadow (PKP). -- Hildesheim, 20 km E, roadside (PKT). -- Weener, 5km W, meadow (PKQ). -- Verden, 1 km S, wet meadow (PKR). -- Wischhafen, roadside (PKO). -- N o r d r h e i n - W e s t- f a l e n. Bechum, bank of small stream (PKV). -- Burscheid, 4 km SE, meadow (PKX). -- Kamen, roadside (PKY). -- Lahde, 10 km S, roadside (PKU). -- R h e i n l a n d - P f a l z. Hermeskiel, 2 km N, meadow (PLC). -- Kastellaun, 3 km SW, edge of Picea forest (PLB). -- Koblenz, Rhenz, roadside (PLA). -- Saarborg, 2 km W, dry meadow (PLD). -- S a c h e n - A n h a l t. Near Dessau, (PMYD^{x}). -- Lausitz near Löbau, (PMYC^{x}). -- S c h l e s w i g - H o l s t e i n. Bredstedt, 5 km S, roadside (PKB). -- Entin, Gross Timmendorf, roadside (PKL^{x}). -- Elmenhorst, wet meadow (PKJ). -- Flensburg, 3 km E (PKA). -- Husum, 5 km N, meadow

(PKC). -- Kiel, Laboe (PKG^{x}). -- Kitzeberg at Kiel, (PMYA^{x}). -- Lauenburg, bank of Elbe (PMH^{x}). -- Lauenburg, Gross Disnach, roadside (PKM^{x}). -- Lauenburg, Gross Disnach, 2 km N, dry meadow (PKK^{x}). -- Lübeck, Pogeez, roadside (PKN^{x}). -- Meldorf, bank of small stream (PKD). -- Meldorf, 10 km S, bank of small stream (PKE). -- Neustadt, 2 km NW, sandy soil (PKH^{x}). -- Wewelsfteth, bank of Stör (PKF). -- B e r l i n. Wittenau, wet meadow (PMO^{x}). -- B r a n d e n b u r g. Eberswalde, Berggieshübel, Zwiesel (PMM^{x}). -- Gransee, 5 km N (PMN). -- M e c k l e n b u r g. Lanenburg, Blankensee, roadside (PML^{x}). -- Greifswald, 2 km N (PMK^{x}). -- Mesenkenhagen, wet meadow (PMP). -- Rügen, (PMJ^{x}). -- S a c h s e n - A n h a l t. Bitterfeld, Zschornewitz 300 m (PMS^{x}). -- Finne, Bad Bibra (PMT^{x}). -- Hecklingen, Lindich, edge of forest (PMV). -- Ohmgebirge, Geschwende (PMU^{x}). -- Saale, (PMR^{x}). -- T h ü r i n g e n. Hermesdorf, (PMQ^{x}).

GREAT BRITAIN. 2n=28 E n g l a n d. At Astley, (PGR^{x}). -- Cambridgeshire, Hirston, edge of Wicken Fen (PGP). -- Cheshire, Capenhurst (PGK^{x}). -- Cheshire, Mere (PGM^{x}). -- Golborne, (PGT^{x}). -- Huntingdonshire, St Neots (PGO^{x}). -- Leigh, (PGQ^{x}). -- At Leigh Soil, on stiff clay (PGS^{x}). -- Shropshire, Lee (PGN^{x}). -- N o r t h e r n I r e l a n d. Anthrim, Belfast, bank of Lagan (PGF^{x}). -- Anthrim, Belfast, Legoniel, roadside (PGG^{x}). -- Anthrim, Doagh, meadow (PGH^{x}). -- Down, Crossgar, roadside 100 m (PGJ^{x}). -- S c o t l a n d. Aberdeenshire, Braemar, bank of small stream 350 m (PGB). -- Aberdeenshire, Bucksburn, roadside (PGD). -- Aberdeenshire, Oldmeldrum, dry meadow on slope 100 m (PGC). -- Orkney, St Ola, Scape, roadside (PGA^{x}). -- Peebles, Innerleithen, river bank (PGE). -- W a l e s. Carnarvon, Dolwyddelan, roadside 325 m (PGL^{x}).

HUNGARY. 2n=14 B u d a p e s t (district 13). Gödöllö, (POX^{x}). -- Pilisvörösvar, (POY). -- D e b r e c e n (district 8). Hajdúszoboszló, 50 m (POV). -- G y ö r (district 7). Győr, 5 km E, roadside (POT). -- S z o l n o k (district 10). Szolnok, 10 km E, wet meadow (POU).

ICELAND. 2n=14 I s a f j a r d a r S y s l a. Haukadalur, Biskupstungur, Árnessý sla (PAA).

ITALY. 2n=14 F r i u l i V e n e z i a G i u l i a. Cervigano del Friuli, 5 km W, bank of small stream (PVX). -- Casarsa, wet meadow (PVR). -- Dogna, (PVQ^{x}). -- Dolo, 1 km N, bank of small stream (PVT). -- Dona di Piave, 8 km S, bank of small stream 1 m (PVU). -- Forni di Sotto, (PVP^{x}). -- Gorzia, 8 km S, dry slope (PVS). -- Udine, Búttrio 90 m (PVV^{x}). -- Udine, Povoletto, 150 m (PVC^{x}). -- L o m b a r d i a. Breno, Croce Domini, wet meadow 950 m (PVK). -- Brescia, Breno, wet meadow 600 m (PVJ). -- Brescia, Valvestino Torano, tall-herb meadow 750 m (PVL). -- Casazza, 3 km SW, Bergamo, bank of small stream 300 m (PVM). -- Valtellina, Sondrio (PVH^{x}). -- P i e m o n t e. Vercelli, Bollengo, wet meadow 250 m (PVG). -- T r e n t i n o A l t o A l d i g o. Sarcke, tall-herb meadow (PVO). -- Schlern, Uri, meadow on sand (PVN).

2n=28 V a l l e d 'A o s t a. Col du Petit St Bernhard, 2 km SW of la Thuile, alpine meadow 1725 m (PVD). -- Col du Petit St Bernhard, la Thuile, alpine meadow 1425 m (PVE). -- Gran Paradiso, (PVF^{x}).

THE NETHERLANDS. 2n=14 D r e n t h e. Beilen, 2 km V, roadside (PHF). -- Vries, canal bank (PHE). -- F r i e s l a n d. Frankener, 1 km N, river bank (PHB). -- Oosterbierum, 2 km NW, the inner dunes (PHA). -- Sneek, 4 km W, bank of small stream (PHD). -- Winsum, bank of small stream (PHC). -- L i m b u r g. Heerlen, (PHV^{x}). -- N o o r d B r a b a n t. Breda, Rijsbergen, roadside (PHT). -- Geertruidenberg, 2 km S, river bank (PHS). -- Gornickem, 7 km SW, canal bank (PHR). -- N o o r d h o l l a n d. Egmond aan den Hoef, 1 km N, canal bank (PHH). -- Hoofddorp, roadside (PHJ). -- Katwijk, 1 km N, roadside (PHN). -- O v e r i j s s e l. Meppel, bank of Meppeler-diep (PHG). -- Vollenbove, (PHX). -- Z u i d h o l l a n d. Gorinchem, 7 km NW, canal bank (PHQ). -- Zegwaard, 6 km N, roadside (PHP).

2n=28 N o o r d h o l l a n d. Haarlem, Vogelenzang, canal bank (PHK). -- Haarlem, Vogelenzang, the inner dunes (PHL). -- Z u i d h o l l a n d. Noordwijk, the inner dunes (PHM). -- Wassenaar, Kijfhoek, the inner dunes (PHO).

NORWAY. 2n=14 A k e r s h u s. Aarnes, bank of the Vorma (PAJ). -- A u s t - A d g e r. Tvedestrand, seashore (PAE). -- B u s k e r u d. Fiskum, 2 km N, the border of a cultivated area (PAD). -- H e d m a r k. Veldre, shore of Mjösa (PAI). -- M ö r e o g R o m s d a l. Åndalsnäs, bank of small stream (PAB). -- Molde, Länset, shore meadow (PAF). -- Sunndal, roadside (PAG). -- O p l a n d. Dovre, Kongsvoll, Kongeveje, wet meadow 1000 m (PAH). -- T r o m s. Tromsöysund herred, Röstbakken (PAC).

POLAND. 2n=14 P o z n a n. Odolanów, roadside (POC^{x}). -- Wronki, meadow (POB^{x}). -- S t e t t i n. Insula, (POA^{x}). -- W a r s z a w a. Pruszków (POD^{x}). -- W r o c l a w. Nowa Ruda, (POH^{x}).

ROUMANIA. 2n=14 B r a ş o v. Codlea, 3 km NW, edge of Quercus forest (PUL). -- Fageras, 1 km E, wet meadow (PUJ). -- Orlat, wet meadow (PUG). -- Sercaia, 4 km NE, wet meadow (PUK). -- Sibiu, 20 km S, wet meadow (PUH). -- C l u j. Aiud, 4 km N, edge of Quercus forest (PUC). -- Ciucea, wet meadow (PUB). -- H u n e d o a r a. Hateg, wet meadow (PUF). -- O r a d e a. Oradea, 15 km E, wet meadow (PUA). -- P i t e ş t i. Rimnicu Vîlcea, Gurăno, edge of Quercus wood (PUN). -- P l o e s t i. Gaesti. 6 km N. edge of Quercus wood (PUO). -- Ion Luca Caragiale, wet meadow (PUP). -- Sinaia, edge of Quercus wood (PUQ). -- T â n g u M u r e s. Mtii Bucegi, Poiana Stînei 1200 m (PUM^{x}). -- T i m i ş o a r a. Caravan, 4 km W, wet meadow (PUE). -- Şag, wet meadow (PUD).

SPAIN. 2n=28 C a t a l o n i a. El Sallent de Sta. Pau, dry meadow 350 m (PUU). -- G r a n a d a S i e r r a N e v a d a.

Barranco de las Viboras, by a little stream 1650 m (PUY). -- Plan Municipal de Sierra Nevada, meadow 2100 m (PUX). -- Plan Municipal de Sierra Nevada, meadow 1800 m (PUV).

SWEDEN. 2n=14 B l e k i n g e. Alnaryd, dry meadow (PCM^{x}). -- Hästholmen, seashore (PCJ). -- Jämjö, Hallarum, tall-herb meadow on the seashore 1 m (PCE). -- Jämjö, Hallarum, Betula wood 10 m (PCD). -- Lösen, Kropp, meadow (PCF). -- Malkvarn, seashore (PCH). -- Märserum, 3 km SO, wet meadow (PCN). -- Stora Hylteskär, seashore (PCK). -- Stora Hylteskär, meadow on the seashore (PCL). -- G o t l a n d. Ardre, Ljugarn, 2 km N, seashore (PBY^{x}). -- Burgesvik, 2 km S (PDYG). -- Fårön, Ullahau, the inner dunes (PDYF). -- G ä v l e b o r g. Anundsjö, near the church (PDYD). -- Hamrånge, Axmarby, meadow (PBG). -- Ljusdal, Måga at the SW part of Växnan, shore (PBF). -- Kungsfors, (PDR). -- Gävle, Stigslund, edge of Populus forest (PDS). -- Gävle, Stigslund, tall-herb meadow (PDT). -- Gävle, Stigslund, roadside (PDU). -- Gävle, Stigslund, in a Picea forest (PDV). -- Gävle, Stigslund, Apotekarevreten, bank of small stream (PDX). -- Gävle, Stigslund, meadow (PDYA). -- Östrafärnebo, tall-herb meadow (PBK). -- G ö t e b o r g o c h B o h u s. Grundsund, 0,5 km W, seashore (PBR). -- Marstrand, 2 km N (PBS). -- Sannäs, 1 km N, meadow (PBO). -- Skee, 5 km SW (PBN). -- Uddevalla, Kuröd, meadow (PBP). -- Uddevalla, Nedre Bräcke, bank of shell-rich gravel (PNQ). -- H a l l a n d. Skärbäck, meadow on the shore of Skärsjön (PDYS). -- J ö n k ö p i n g. Vireda, roadside (PDYJ). -- J ä m t l a n d. Sunne, Vällviken, shore (PBB). -- K a l m a r. Borgholm, Rosentorp, bank of small stream (PCA). -- Målilla, Emmenäs, on bank of the Emån (PDYP). -- Torslunda, Lenstad, seashore (PCB). -- Tvärskog, Betula wood (PCC). -- Öland, Solberga, meadow by the Baltic (PDYE). -- K o p p a r b e r g. Lima, Åkra, meadow (PDYB). -- Lima, Åkra, Åkerbyn, 2 km N (PDYC). -- Orsa, Bäcka, shore (PBH). -- Siljansnäs, Alvik (PBJ^{x}). -- K r i s t i a n s t a d. Arkelstorp, 2 km SE, roadside (PCR). -- Benestad, tall-herb meadow (PDK). -- Hammarsjön, Hovby, tall-herb meadow (PDA). -- Hanaskog, the

limestone quarry (PCQ). -- Ivön, Ivö klack, wood (PCS). -- Ivön, Söndremark, edge of Fagus forest (PCT). -- Kiaby, roadside (PCV^{x}). -- Kiaby, 2 km SE, tall-herb meadow (PCY). -- Lövedal, tall-herb meadow (PCU). -- Staversvad, wet meadow (PCP). - S. Mellby, 100 m (PCX^{x}). -- Trolle-Ljungby, Skaftet (PDB^{x}). -- M a l m ö h u s. Fågelsång, edge of wood (PDJ). -- Genarp, Möllehejdehus, tall-herb meadow (PDH). -- Landskrona, dry meadow 5 km (PDD^{x}). -- Mölle, seashore 1 m (PCO). -- Skurup, Lemneström, marshy land (PDQ). -- S. Sandby, Linnebjär, meadow (PDG). -- Stångby, meadow (PDF). -- Trolleholm, 1 km NW, bank of Saxån (PDE). -- Ven, seashore (PDC^{x}). -- Ystad, Kabusa, seashore (PDL). -- N o r r b o t t e n. Nederluleå, S. Sundlebyn, Näset, dry meadow (PBA). -- S ö d e r m a n - l a n d. Rönö, Sofielund (PDYH). -- S t o c k h o l m. Rådmansö, Norrpoda, shore (PBL). -- Stockholm, St. Skuggan (PBM^{x}). -- V ä r m l a n d. Arvika, Brunsberg, roadside (PDYQ). -- Karlskoga, Degerfors, Sveadallen, roadside (PDYR). -- V ä s t m a n - l a n d. Harbonäs, shore of Tämnaren (PDO^{x}). -- U p p s a l a. Fälaren, meadow (PDM). -- Knivstasjön, Oxhagen (NE Skyttorp) (PDN^{x}). -- Söderfors, meadow on bank of Dalälven (PDP). -- V ä s t e r n o r r l a n d. Arnäs, 1 km NE, tall-herb meadow 25 m (PBS). -- Härnösand, Härnön, Specksta, roadside (PBD). -- Stöde near church, bank of Ljungan (PBE). -- Ä l v s b o r g. Alingsås, Hjälmered, roadside (PBT^{x}). -- Gullered, 1 km W (PBV). -- Ulricehamn, roadside (PBU^{x}). -- Ö r e b r o. Degerfors, Sveafallen (PDYT). -- Ö s t e r g ö t l a n d. Boxholm, Åsbo, Pålsbo, dry meadow (PDYM). -- Hackelboö in the lake Järnlunden (PDYO). -- Hallstad. Kinda, Rimforsa, meadow near Järnlunden (PDYK). -- Kisa, Misterfall, meadow (PDYL). -- Vadstena, 2 km S, meadow (PBX). -- Ödeshög, Sättra, meadow (PDYN).

2n=21 B l e k i n g e. Lösen, Kropp, wet meadow (PCG).

SWITZERLAND. 2n=14 B e r n. Eblingen, meadow 650 m (PSA). -- Grund, 2 km SE 1300 m (PRY). -- Gümmenen, roadside 500 m (PRT). -- Oberwil, 5 km E, tall-herb meadow 800 m (PRU). -- Saanemöser, wet meadow 1000 m (PRV). -- Simmenthal, Lenk, dry meadow on limestone 1100 m (PRX). -- Sustenpass, Gadmen, 3 km E, roadside 1500 m (PSC). -- Sustenpass, Nessenthal, 2 km W, meadow 900 m

(PSB). -- F r e i b o u r g. Ogoz, 5 km E, roadside 700 m (PRS). -- G r a u b ü n d e n. Laret-Davos, Stützbach, alpine meadow on limestone 1500 m (PSJ). -- N e u c h â t e l. Rochenfort, 1 km E, roadside 750 m (PRL). -- Ste-Croix, 1035 m (PRN). -- S c h w y z. Rothenthurm, 8 km SW, tall-herb meadow 850 m (PRK). -- Steinen, 2 km N, tall-herb meadow, 850 m (PRJ). -- U r i. Altdorf, 2 km S, bank of Reuss 475 m (PSF). -- Sustenpass, Meiendörfli, 2 km SE, roadside 1200 m (PSE). -- V a u d. Col du Pillon, roadside 1550 m (PRQ). -- Lac de Joux 1000 m (PSK^{x}). -- Rennaz, wet meadow 350 m (PRR). -- Vuiteboeuf, in the Jura, roadside 900 m (PRO). -- Z ü r i c h. Lägern (PSM^{x}). -- Lägern, Niederweniigen, wet meadow, on limestone 775 m (PRBA). Lägern, Niederweniigen, headland 760 m (PRBB). -- Lägern, Niederweniigen, meadow 745 m (PRBC). -- Lägern, Niederweniigen, clayey field 730 m (PRBD). -- Lägern, Niederweniigen, forest 715 m (PRBE). -- Lägern, Niederweniigen, edge of wood 695 m (PRBF). -- Lägern, Niederweniigen, forest 675 m (PRBG). -- Lägern, Niederweniigen, forest 660 m (PRBH). -- Lägern, Niederweniigen, edge of the wood 655 m (PRBI). -- Lägern, Niederweniigen, tilled field 640 m (PRBK). -- Lägern, Niederweniigen, wet meadow 630 m (PRBL). -- Lägern, Niederweniigen, tilled field 600 m (PRBM). -- Lägern, Niederweniigen, roadside 560 m (PRBN). -- Richterswil, tall-herb meadow 500 m (PRG). -- Rümlang, Petri, dry meadow (PR[illegible]). -- Schlieren, roadside (PRH^{x}). -- Siglistorp, tall-herb meadow (PRA). -- Tägerwilen, dry meadow (PRC). -- Wagen, meadow (PRE). -- Zollikon, Girstel, dry meadow (PRF).

2n=28 N e u c h â t e l. Fleurier, in the Jura, roadside 250 m (PRM). -- Z ü r i c h. Lägern (PSM^{x}). -- U r i. Andermatt, alpine meadow 1450 m (PSH). -- Urserental, Hospenthal at the Reuss, meadow 1550 m (PSG). -- V a l a i s. Champes-Lac, 1400 m (PSD^{x}). -- Champex, alpine meadow 1500 m (PSL^{x}). -- V a u d e. Rolle (PRP).

USSR. 2n=14 K u y b y s h e v. Kashpiroka, bank of Volga (POP). -- L a t v i a. Riga, Salaspils (POK^{x}). -- L e n i n g r a d. Leningrad, 10 km S, at Neva (POS). -- L i t h u a n i a. Kaunas, (POL^{x}). M e n s k. Gomel, near Brest (PON^{x}). -- Zaslavi, (POM^{x}). -- S t a v r o p o l. Ispravnaya, Caucasi, alpine meadow 2000 m (POQ^{x}). -- U k r a i n e. Lwow, (POO^{x}).

YUGOSLAVIA. 2n=14 B o s n a i H e r c e g o v i n a. Jabuka, bank of small stream (PYG). -- Ljubogosca, 2 km E, wet meadow 875 m (PYE^{x}). -- Konjic, 5 km W, meadow (PYH^{x}). -- Ljubogosca, 4 km W, meadow 915 m (PYB). -- Ljubogosca, roadside 825 m (PYC^{x}). Ljubogosca, by small stream (PYYB). -- Ljubogosca, 10 km NE, roadside 1125 m (PYD). -- Olov, 3 km SW, headland 950 m (PXY^{x}). -- Prenj planina, Ruji ište, dry slope (PYJ). -- Romänja, meadow 1390 m (PYF). -- Sarajevo, the mountain Trebević, meadow 840 m (PYA). -- Tuzla, roadside 400 m (PXV). -- Zvornik, 8 km W, dry slope 550 m (PXX). -- C r o a t i a. Bos. Šamac, 10 km NE, roadside (PXL). -- Brušane, limestone headland 600 m (PXS^{x}). -- Costa Karlobag, 10 km E, roadside on limestone 940 m (PXT^{x}). -- Karlovac, 12 km N, roadside (PXN). -- Krnjak, 3 km N, meadow (PCQ). -- Novi Marof, 4 km S, meadow 200 m (PXF). -- Novska, bank of small stream (PXH). -- Okoli, edge of Quercus forest (PXG). -- Okućani, 2 km S, (PXJ). -- Orjava, roadside (PXK). -- Slunj, 4 km N, dry meadow (PXP^{x}). -- Vrhovine, 10 km E, wet meadow 700 m (PXR). -- Župania, 20 km E, Quercus forest (PXM). -- S e r b i a. Bioska, dry slope (PYN). -- Cajětina, meadow on serpentine (PYP). -- Cajětina, alpine meadow 900 m (PYO). -- Kragujevac, Grošnica, Quercus wood (PYM). Kragujevac, Grošnica, roadside (PYYA). -- Kuršumlija Banja, roadside 350 m (PYT^{x}). -- Sarajevo, Mokra Gore (PYX). -- Orašje, 2 km N 100 m (PYL). -- Soko Banja, Ozren, roadside 410 m (PYR). -- Soko Banja, Ozren, meadow 700 m (PYS). -- Vranje, 500 m (PYU). -- Vranje, Kriva Feja 1000 m (PYV). -- Vršac, 4 km SW, wet meadow (PYK). -- Zeoke, Quercus wood (PYQ). -- S l o v e n i j a. Čatež, tall-herb meadow (PYM). -- Istra, Rupa (PXC). -- Ljubljana, 10 km SW, roadside (PXA^{x}). -- Loka, 3 km SE, roadside (PXE). -- Radohova, 5 km SW, meadow 280 m (PXD^{x}). -- Storje, meadow (PXB).

2n=28 C r o a t i a. Cricvenica, 1 km NW, dry meadow (PXQ). -- Zadar, bank of river 90 m (PXU).

Lathyrus binatus Pančić

YUGOSLAVIA. 2n=14 B o s n a. Ljubogošca, 2 km E, scree slope (BAD). -- Ljubogošca, 4 km W, scree slope 800 m (BAC). -- Sarajevo monte Castello, scree slope 770 m (BAB). -- Sarajevo, Mostainicaschlukt, scree slope (BAF). -- Sarajevo Trebević, scree slope 850-900 m (BAA). -- S e r b i a. Mokra Gora, scree slope (BAE).

Lathyrus hallersteinii Baumg.

ROUMANIA. 2n=14 B r a ş o v. Orlat, north slope of Quercus wood 500 m (HAG). -- Sibiu, Csora (Cioara, Cisnădie), north slope of Quercus wood (HAH). -- C l u j. Aghires, Quercus wood 500 m (HAA). -- Faget, Quercus wood 600 m (HAB). -- Turda Cheizii, Quercus wood 800 m (HAC). -- H u n e d o a r a. Cilnic, 2 km S, edge of Quercus wood 450 m (HAF). -- Deva, 1 km NW, slope of Fagus forest 450 m (HAD). -- Gura Zlata, 13 km N, steep slope with scrubs 600 m (HAE). -- P i t e ş t i. Rimnicu Vilcea, 2 km E, Quercus wood 500 m (HAK). P l o e s t i. Sinaia, edge of Quercus wood 800 m (HAJ).

YUGOSLAVIA. 2n=14 S e r b i a. Kragujevac, Grošnica, Quercus forest 450 m (HBC). -- Ozren, Soko Banja, slope with scrubs 400 m (HBD). -- Ozren, Soko Banja, Fagus forest 725 m (HBE). -- Priština, Quercus forest on easterly slope 600 m (HBF). -- Titovo Užice, 7 km NW 600 m (HBA). -- Zeoke, 10 km SW Čacak, Quercus forest 500 m (HBB).

APPENDIX II HERBARIUM MATERIAL

Lathyrus binatus Pančić

YUGOSLAVIA. B o s n a. Banja Luka, Hofman (SARA). -- Banjaluka, Hoffman 1879 (SARA). -- Miljacka Schlücht bei Sarajevo, Curčić 1893 (SARA). -- Miljackatal bei Sarajevo, Janchen 1906 (WU). -- Mostainicaschlukt bei Sarajevo, Beck 1885 (PRC). -- Sarajevo, Breindl 1893 (W). -- Sarajevo, Curčić 1899 (W). -- Sarajevo, Gilliat-Smith 1931 (K). -- Trebević bei Sarajevo 1050 m, Maly 1899 (LD, W). -- Trebević 800 m Maly 1901 (C, WU). -- Trebević bei Sarajevo 1050 m, Maly 1904 (L, LD O). -- Westseite des Draguljevac am Trebević 1050 m, Maly 1904 (SARA). -- Nächst der Ziegenbrücke an Füsse des Trebević 600 m, Maly 1911 (SARA). -- Westabhang der Čotina Kapa an Trebević 860-920 m, Janchen 1906 (SARA). -- Nordabhang des Trebević 1300 m, Zerny 1929 (W). -- Zviezda (Drina) in mt Vidača, Šoška 1912 (CL). -- H e r c e g o v i n a. Bešike supra val Drežnica, Vandas 1913 (PR). -- Mt Lupoglav supra Police dictum copiose 1500 m, Vandas 1893 (PR, PRC, SARA). -- Prenj, mt Lupoglav supra Police prope Mostar rarus 1600 m, Vandas 1893 (BP, K, WU). -- Prenj, mt Lupoglav copiose 1800 m, Vandas 1893 (K, W). -- Prenj, Schneider 1911 (W). -- Strmoglavica pl supra val Drežnica, Vandas 1910 (PR). -- S e r b i a. Mokra Gora, in rupestris aridis, Bornmüller 1887 (PRC).

Lathyrus hallersteinii Baumgarten

HUNGARIA. P e s t. Ócsa, Müller 1856 (BP).

ROUMANIA. B r a s o v. Făgăras, Sinca-Nowă, Traian 1950 (CL). -- Făgăras Sinca-Nowă, Tretuit 1950 (CL). -- Götzenberg ad N'Driomo'd, com. Cibinensis, Thaisz 1894 (BP). -- Göttzenberg, Ernöi 1895 (BP). -- Götzenberg, com. Szeben, Ernöi 1896 (BP). -- Hammersdorf bei Hermanstadt (Sibiu), Kayser 1845 (W). -- Hammersdorf bei Hermanstadt, Dörfler 1885 (BP, FI, GB, PRC, W). -- Heldenburg, Römer 1888 (CL). -- Hermansdorf, Schur (K, W). -- Hermanstadt (W). -- Hermanstadt, Schur (BP, PRC). -- Hermanstadt, Schur 1853 (W). -- Hévy (Heviz, Hogniz), Baumgarten 1809 (CL). -- Hévy, Baumgarten 1811 (W). -- Hévy, Baumgarten 1817 (W). -- Kronstadt (Brasov), Römer 1906 (CL). -- Michelsburg (Mica), Barth 1881 (UPS). -- Michelsburg, Michfuss (W). -- Nagy Szeben (Sibiu), Schneider 1914 (W). -- Orlat 500 m,

Barth 1905 (PRC). -- C l u j. Mt Apuseni Lunca Ampoitei cheile Ampoitei, Pop 1959 (CL). -- Bükk, Kolozsvár (Cluj), 1905 (GB). -- Bükk, Kolozsvár, Petrak 1905 (PRC). -- Mt Bükk bei Kolozsvár, Sufó 1905 (BP, CL, FI, G, GB, H, O, PR, W, WU). -- Bükk, Richter 1905 (PR). -- Claudiopoli (Cluj), Wolff (CL, K). -- Clausenburg (Cluj), Wolff (W). -- Clausenburg, Hoja, Janka 1855 (FI). -- Clausenburg, Hoja 500 m, Schur 1883 (CL). -- Cojočna inter Gărbău et Cluj, Nyárády 1923 (CL). -- Cojočna Făget, mt Peana 700-800 m, Nyárády (CL). -- Făget,600 m, 1910 (BP, BUC, G, GE, GE, H, LD, O, WU). -- Kis-Fenes (Floreşti), (CL). -- Kolos (Cluj), Freyn 1871 (CL). -- Kolozs, Varerdő supra Gyalu, Soó 1941 (CL). -- Kolozsvár (Cluj) mt Hoja, Soó 1941 (CL). -- Plecskavölgy (Valea Plecica), Richter 1901 (CL). -- Somesul Cal'd, Barth 1882 (W). -- Szent László (Săvădisla), Baumgarten 1834 (CL). -- Torda 600 m, 1816 (L, WU). -- Torda 600 m, Wolff & Wolff 1816 (BM, BP, FI, H, L, PR, PRC, W, WU). -- Torda, 1888 (WU). -- Torda-Aranyos, Borev, Borzy (BP). -- Torda-Aranyos, Medény, Haynald 1863 (BP). -- Torda-Aranyos, Toroczkó-Szent-György, Csató 1874 (BP). -- Torda-Aranyos, Varfalva, Haynald 1862 (BP). -- Torda, Gulinsche, Hazadék, 1908 (BP). -- Turda, Wolff & Wolff 1882 (GB). -- Turda 600 m, Wolff & Wolff 1888 (CL). -- Turda, Nagy 1901 (BP, CL). -- Turda bei Alsrud, Bainjai 1909 (CL). -- Turda, Belioara 1200 m, Seran 1950 (CL). -- Turda mt Măgura supra Sălicea 800-820 m, Nyárády 1930 (CL). -- H u n e d o a r a. Csora (Cioara), Baumgarten 1 29 (W). -- Deva, Barth 1883 (PRC) -- Deva Cluj 1910 (FI). -- Deva Olim, Richter 1910 (BP, G, GB, W). -- Deva Olim, 1910 (GB). -- Dobra, Barth 1882 (UPS). -- Efdély, Csató 1866 (BP). -- Efdély, Hátszeg (Hateg), Csató 1870 (BP). -- Kelnek (Călnic), Csató 1873 (WU). -- Retezat mt Fata Feti supra Gura Api, 1200-1600 m, Nyárády 1925 (CL). -- Retezat, Gura Zlata, Riu Mare 600-800 m, Scheffer 1935 (WU). -- Retezat, mt Ptr. Măcestilor supra Parospestera, 900-1000 m, Nyárády 1930 (CL). -- Retezat, Riu Mare, Bogsch & Günter 1914 (CL). -- Sacaramb 700-800 m, Soran 1951 (CL, L, P). -- P l o e s t i. Sinaia, Loitlesberger (W). -- Sinaia Prahova, Hertz-Berger (W). -- T i m i s o a r a. Banat, Heuffel (W, UPS). -- Banat Plavischevitza, Borbás 1873 (WU). -- Banatus mt Do (W). -- Banatus Plavischevitza vallis Kazan, Simkovics 1874 (BP). -- Banatus Swinitza bei Danutium, Borbás 1873 (FI). -- Banatus, Heuffel (LD, UPS). -- Baile Herculane,

Borza 1920 (CL, GB). -- Herculis (Herculesbad), Degen (BM, BP, G, LD, M, PR, PRC, W, WU). -- Herculis, Dorner 1835 (UPS). -- Herculis, Borbás 1873 (BM, BP, W, WU). -- Herculis, Eovurt 1878 (FI). -- Herculis, Swinkovics 1874 (BP, CL). -- Herculis, mt Domugled, Degen 1887 (W). -- Mt Domogled supra Herculesfürdö, 1000 m, Kárpáti 1937 (PRC). -- Krassó-Szörény (Banat) mt Domogled, Herculesfürdö (Herculis) 1000 m, 1937 (PR). -- Krassó-Szörény, Herculesfürdö, mt Domogled, Wierzbicki (PRC, CL). -- Zvidovar, Heuffel (CL). -- Herculesbad, Krasso'h, Wanger 1905 (GB). -- Herculesbad (Herculis), Maierhof 200 m, Baenitz 1895 (BP, CL, FI, G, H, L, PR, PRC, W, WU). -- Krasso'h prope Herculesbad, Wanger 1905 (GB). -- Herculesbad, Wetschky 1889 (FI). -- Herculesbad, Schneider 1909 (BM, G, L, P, W). -- Herculesbad, Suscului, Watzl 1909 (WU). -- T r a n s s y l v a - n i a. Baumgarten (PRC, W). -- Schur 1854 (CL). -- Barth 1874 (WU).

POLAND. W a r s z a w a. Bug, Zajecniki bei Losice, Karo 1873 (FI).

YUGOSLAVIA. S e r b i a. Ilič 1889 (WU). -- Südserbien, Ilič (GB). -- Vukmanovo (Gadzin Han), Ilič (W). -- Brdo, Zitnog Potoka bei Prokuplje, 1911 (BEO). -- Friedrichsthal, Bilo (W). -- Friedrichsthal, Gozel (W). -- Gabrovac, Ilič 1889 (SARA, WU). -- Kragujevac Drača, 1940 (BEO). -- Kragujevac Grošnica, 1939 (BEO). -- Manastir Subhodol nei Kraljevoselo, Ilič 1899 (SARA). -- Niš, Suvódol, Vetrovic 1886 (WU). -- Niš, Ilič 1889 (PRC, W, WU). -- Niš, Adamovic 1896 (LE, W). -- Pirot, Ilič (W). -- Prokuplje, Ćukovaca 1911 (BEO). -- Mt Rtanj, Ilič 1890 (SARA). -- Mt Rtanj supra Alessinoe, Soška 1923 (W). -- Mt Seličevica, Ilič (PRC). -- Stara Planina, Pirot, Dugo Bilo, 1958 (BEO). -- Stara Planina, Pirot, Rišor, Zubersui Rt. 1958 (BEO).

Borra 1920 (Cl, GB). — Heroulia (Heroulesbad), Degen (HM, BP, G, LD, M, Sa, PRO, K, WU). — Heroulia, Porser 1895 (UPS). — Heroulia, Borbás 1872 (SM, BP, W, WU). — Heroulia, Szovát 1878 (PI). — Heroulia, Swinkovics 1874 (BP, Cl). — Heroulia, mt Domugled, Degen 1897 (W). — Mt Domogled supra Heroulesfürdő, 1000 m, Kárpáti 1937 (PRO). — Krassó-Szörény (Banat) mt Domogled, Heroulesfürdő (Heroulia) 1000 m, 1937 (PM). — Krassó-Szörény, Heroulesfürdő, mt Domogled, Wierzbicki (PRO, Cl). — Sylvover, Heuffel (Cl). — Heroulesbad, Krasso'n, Wanger 1905 (GE). — Heroulesbad (Heroulia), Malerhof 200 m, Baenitz 1895 (BP, Cl, PI, G, H, L, PR, PRO, W, WU). — Krasso'n prope Heroulesbad, Wanger 1905 (GE). — Heroulesbad, Wetschky 1889 (PI). — Heroulesbad, Schneider 1909 (BM, O, L, P, W). — Heroulesbad, Simonkai, Wahl 1909 (WU). — T r a n s s a y l v a n i a. Feumgerten (PRO, W). — Sonnr 1854 (Cl). — Barth 1874 (WU).

POLAND. W a r s z a w a. Sog, Salzsumpf bei Loslow, Karo 1875 (PI).

YUGOSLAVIA. S e r b i a. Ilić 1889 (WU). — Südserbien, Ilić (GB). — Vukasovo (Gržatin Han), Ilić (W). — Brdo, Zitnog Potoka bei Prokuplje, 1911 (BEO). — Friedrichsthal, Sklo (W). — Friedrichsthal, Gossl (W). — Gubrovac, Ilić 1889 (SARA, WU). — Kragujevac Draga, 1940 (BEO). — Kragujevac Gročnica, 1939 (BEO). — Manastir Subotol bei Kraljevosalo, Ilić 1889 (SARA). — Niš, Suvodol, Vetrovic 1888 (WU). — Niš, Ilić 1889 (PRO, W, WU). — Niš, Adamovic 1896 (LE, W). — Pirot, Ilić (W). — Prokuplje, Cukovac 1911 (BEO). — Mt Ržanj, Ilić 1890 (SARA). — Mt Ržanj supra Aleksinac, Sonne 1923 (W). — Mt Selidavica, Ilić (PRO). — Stara Planina, Pirot, Dugo Selo, 1958 (BEO). — Stara Planina, Pirot, Niš, Suberava Rt, 1958 (BEO).